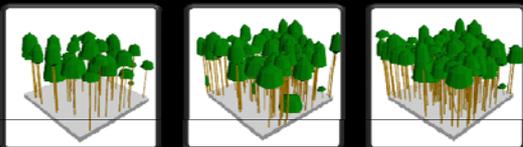


Corso di laurea in SFA e DISMIT
Modulo di ecologia forestale
Anno Accademico 2007-08



Giorgio Vacchiano – Dip. Agr. e Silv. Iler
giorgio.vacchiano@unito.it

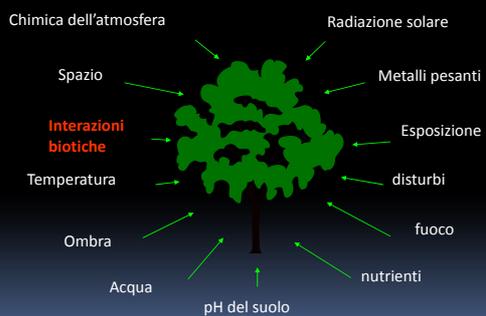
LA COMPETIZIONE IN FORESTA



Contenuti del seminario

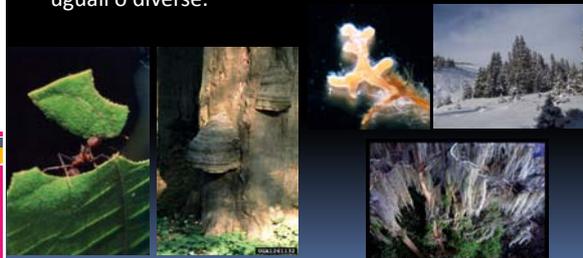
- **La competizione**
 - Definizione
 - Caratteristiche
 - Effetti
 - Ruolo ecologico
- **L'autodiradamento**
 - Definizioni
 - Significato ecologico
- **Misurare la competizione**
- **Gestire la competizione**
- **Prevedere la competizione**

Fattori di crescita



Interazioni biotiche

Lo studio degli ecosistemi è l'analisi delle RELAZIONI tra individui, popolazioni e comunità, di specie uguali o diverse.



Interazioni biotiche

	+	0	-
+	Facilitazione Mutualismo		
0	Commensalismo	(Neutralismo)	
-	Predazione Parassitismo Erbivoria	Amensalismo	Competizione

da Barbour et al. (1999), *Terrestrial Plant Ecology*

Interazioni biotiche

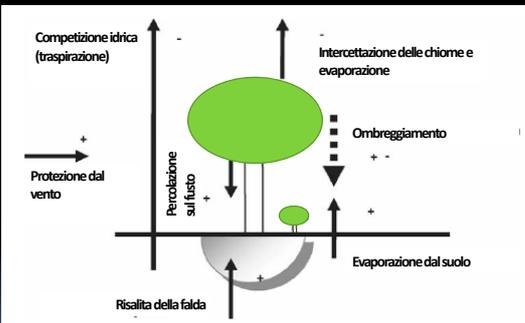
Raramente gli organismi vegetali interagiscono direttamente (v. dopo). Le interazioni sono mediate dall'AMBIENTE.



da Bruno (2003), *Trends Ecol. Evol.* 18



Interazioni biotiche



da Zavala e de la Parra (2005), *Ecological Modelling* 188

La competizione

Interazione tra individui provocata dalla comune domanda di risorse limitate e arrecante una riduzione nella performance dei competitori (accrescimento, sopravvivenza, riproduzione).

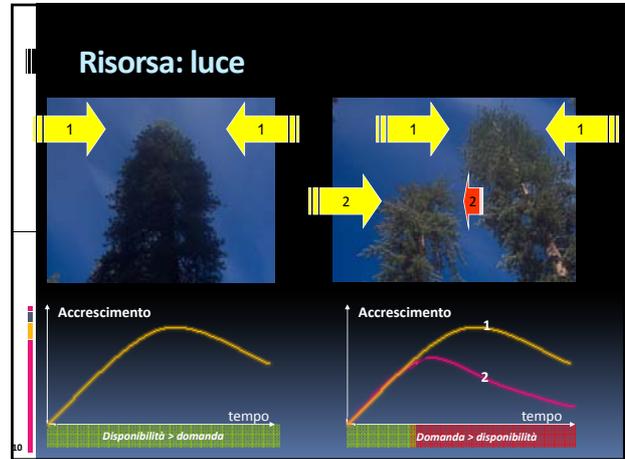
da Begon et al. (1996), *Ecology*

La competizione

Nel mondo vegetale:

- Prossimità, spaziale o temporale
- Risorsa comune non sufficiente ("CUM-petere")
 - Luce
 - Spazio fisico
 - Acqua e nutrienti
 - (riproduttiva)

9

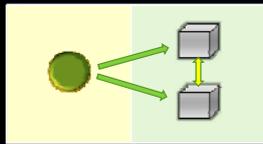


Tipo di competizione

Sfruttamento

- Mediata da risorse
- Stabile o instabile

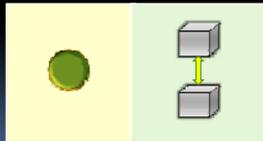
Es. dominanza



Interferenza

- Concorrenza diretta
- Equilibrio stabile

Es. allelopatia



11



Tipo di competizione

Alliaria petiolata (garlic mustard)

©2004 Eliza K. Jewett

da Nuzzo (1999), *Biol.Inv.* 1

Sfruttamento + interferenza
Invasione di 5 m/anno in foreste di latifoglie

Tipo di competizione

Competizione apparente

1. *Botrychium australe* in ambienti aridi
2. Invasione post-incendio di *Agrostis capillaris* (alloctona)
3. Attrazione degli erbivori, che attaccano anche l'arbusto nativo.

da Session e Kelly (2000), *Oikos* 96

Tipo di competizione

SIMMETRICA: ogni individuo riceve una parte di risorse proporzionale alla sua richiesta

ASIMMETRICA: gli effetti della competizione si ripercuotono in modo più che proporzionale su uno dei competitori.

Tipo di risorsa	Localizzazione delle risorse	Caratteristiche individuali
<ul style="list-style-type: none"> • Luce – asim. • Acqua – simm. • <u>Interazioni</u> 	<ul style="list-style-type: none"> • Microstazioni • Morfologia • Spazio & <u>tempo</u> 	<ul style="list-style-type: none"> • Età (dimensioni) • Pool genico • <u>Strategia</u>

15

Community ecology

Competizione

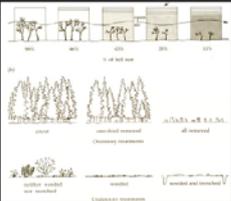
Fertilità	Disturbi naturali	Struttura spaziale
<p>Resource-ratio hypothesis</p> <p>Competizione costante con la fertilità stagionale</p> <p>Equilibrio competizione-epigea-ipogea</p> <p>da Tilman (1987), <i>Func.Ecol.</i> 87</p>	<p>Competition-stress hypothesis</p> <p>Comp. proporzionale alla fertilità</p> <p>Equilibrio competizione-tolleranza allo stress</p> <p>da Grime (1977), <i>Am.Nat.</i> 111</p>	

16

Competition for light and soil moisture (Shirley 1945)



Picea glauca, *Pinus strobus*, *P. resinosa* and *P. banksiana* are the overstory species in north central Minnesota, but they do not reproduce in their own shade. Usually hardwood seedlings will occur beneath the trees.



Objective: determine the relative importance of competition for light and soil moisture to pine seedlings.

- (a) **Effect of competition for light.** Pine seedlings were grown beneath different layers of screens to achieve different levels of sunlight (a). Growth was not satisfactory below about 65% light.
- (b) **Combined effect of shade and root competition for water.**
 - The overstory had three treatments, (b), (uncut, 1/3 removed, and clear cut).
 - The understorey was also varied (control, all understorey plants removed, weeded and trenched to sever plant roots).

The results were complex and appeared to depend on initial site moisture. In moist areas, opening the canopy, weeding, and trenching improved seedling growth. In dry areas opening the canopy decreased seedling survival, but not seedling growth.

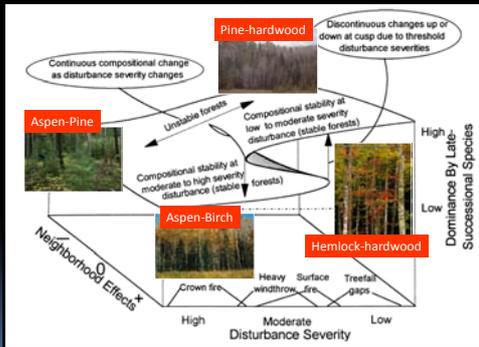
17

Community ecology



18

Community ecology



Continuous compositional change as disturbance severity changes

Unstable forests

Compositional stability at low to moderate severity disturbance (stable forests)

Compositional stability at moderate to high severity disturbance (stable forests)

Discontinuous changes up or down at cusp due to threshold disturbance severities

High

Low

Dominance By Late-Successional Species

Neighborhood Effects

High Disturbance Severity

Moderate

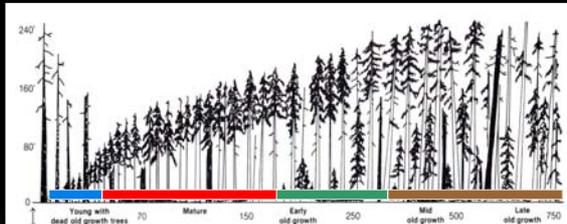
Low

Disturbance Severity

da Frelich & Reich (1999), *Ecosystems* 2

19

Population ecology



STAND INITIATION: tra semenzali e con specie erbacee/arbustive

STAND RE-INITIATION: tra piano dominate e rinnovazione

STEM EXCLUSION: intensa competizione intraspecifica, mortalità

OLD GROWTH: tra piani di vegetazione e specie diverse

20

Strategie competitive (Grime, 1977)

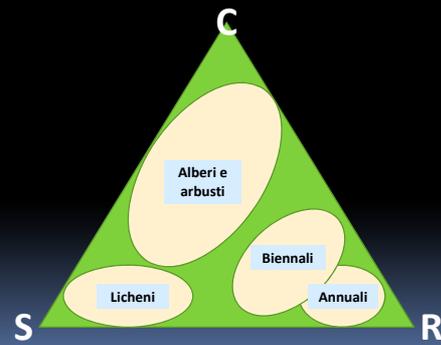
Competitori (C): allocano > risorse all'accrescimento, sfruttando quelle immediatamente disponibili nell'ambiente (alta efficienza)

Stress-tolleranti (S): vivono in ambienti limitanti dove sopravvivono allocando > risorse al mantenimento o alla difesa (es. deserti, tundra, prati alpini)

Ruderali (R): vivono in habitat temporanei e frequentemente disturbati. Allocano > risorse alla riproduzione (es. malerbe)

21

Strategie competitive (Grime, 1977)



22

Examples of C-selected species



Vicia cracca (blue vetch)
www.bruehlmeier.rwth-aachen.de/12011%20Vicia%20cr



Poa pratensis
turfgrassmanagement.psu.edu/ Graphics/ib/ku.jpg

- Allocate most available resources to growth.
- Highly competitive root systems (often rhizomatous species).
- Strong competitors for nitrogen. Or are nitrogen fixers.
- High efficiency for capturing resources (water, light, nutrients) that makes it difficult for other species to compete.

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Examples of S-selected species



Ledum decumbens



Picea mariana



Rhizocarpon geographicum

- Long-lived, slow-growing plants. Often woody. Many lichens.
- Live in sites with low-levels of nutrients.
- Relatively coarse, evergreen leaves or non deciduous structures.
- High levels of tannins and other secondary metabolites. Highly defended against insect attack.
- Tend to have years of high flowering and years of low flowering.

24

Examples of *R*-selected species



Epilobium latifolium



E. angustifolium

- Soft, deciduous leaves, that are poorly defended against insects.
- Produce many flowers. Both produce many light seeds that are easily dispersed by wind.
- Generally short-lived plants that are replaced by other species during succession.

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Attributi della competizione

INTENSITA': impatto assoluto dei competitori sulla pianta soggetto (accrescimento, forma, riproduzione, sopravvivenza).

IMPORTANZA: grado di influenza della competizione rispetto ad altri fattori che determinano la risposta osservata (es. accrescimento) ma sono indipendenti dalla densità.

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Attributi della competizione



Pineta matura a roverella
 Bassa fertilità stagionale (basifila)
 Tessitura a gruppi
 Struttura irregolare
 Competizione epigea+ipogea
Importanza <, intensità > (locale)

Pineta acidofila di invasione
 Alta fertilità stagionale
 Tessitura regolare
 Struttura monoplana
 Competizione per la luce
Importanza >, intensità =

27

Modalità di competizione

È più intensa la competizione interspecifica o quella intraspecifica?

Esclusione competitiva (Gause, 1932)

“Due competitori identici (la cui nicchia ecologica coincide) non possono coesistere se le risorse sono limitate”.

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Modalità di competizione

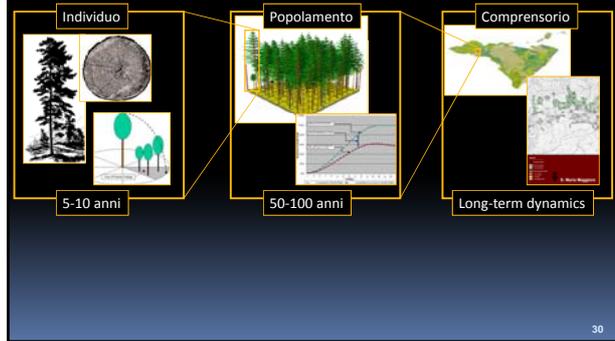
Relazione tra copertura esercitata dagli individui e loro distanza dalla pianta soggetto in 3 specie del Chihuahan Desert, CA.



L'intensità della competizione (decremento della biomassa per unità di distanza) è più elevata tra conspecifici.

da Briones et al. (1996), J.Veg.Sci. 7

Effetti della competizione



Effetti della competizione

INDIVIDUO – BREVE TERMINE:

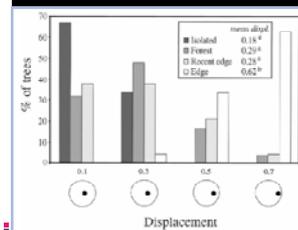
- Morfologia
- Tasso di assimilazione delle risorse
- Allocazione delle risorse (priorità)*
- Accrescimento, biomassa
- Fecondità, riproduzione

2 risposte possibili: plasticità o mortalità

*foglie, organi riproduttivi: alta priorità
fusto, organi di riserva: bassa priorità (+ sensibili)

31

Effetti della competizione



Acer saccharum – Asimmetria di chioma in funzione della densità (foresta chiusa, albero isolato, radura).

(Brisson, 2001: Can.J.For.Res. 31)

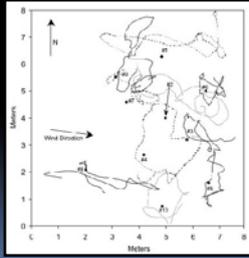
Variazione repentina in Lodgepole pine (*Pinus contorta*).



32

Effetti della competizione

Crown shyness per ombreggiamento (*Dryobalanops aromatica*) o abrasione meccanica (*Pinus contorta*).



da Rudnicki et al. (2001), *Trees* 15

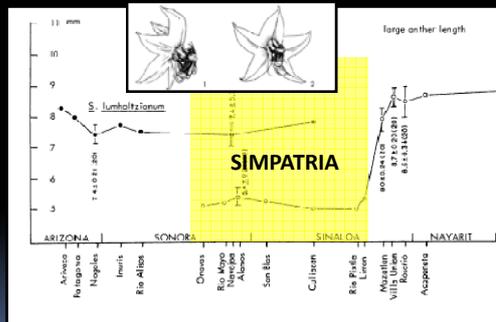
Effetti della competizione

Plasticità: Abilità di alterare il proprio tasso di crescita o la propria morfologia in risposta ai cambiamenti ambientali.

Plasticità "evolutiva" (a lungo termine):

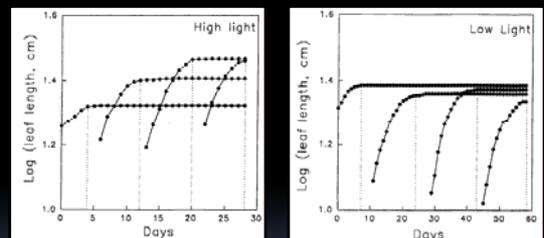
- Tolleranza o adattabilità (sp. euriecie)
- Sfuggenza (spaziale o temporale)
- Segregazione dei caratteri
- Differenziazione della nicchia ecologica (fondamentale vs. realizzata)

Effetti della competizione



da Walen (1978), *Sys.Bot.* 3

Effetti della competizione



Foglie di *Alocasia macrorrhiza* in diverse condizioni di luce

da Sims & Pearcy, (1992), *Am.J.Bot.* 79

Effetti della competizione

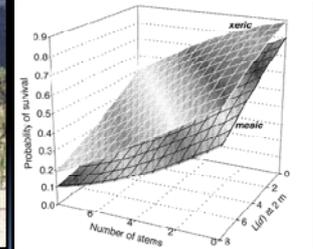
Mortalità: quando la capacità di una pianta di compensare lo stress competitivo con una risposta plastica è superata.



37

Effetti della competizione

Probabilità di sopravvivenza di *Pinus flexilis* in funzione della propria densità (competizione intraspecifica) e di quella di *Abies amabilis* (interspecifica).



da Donnegan & Rebertus (1999), *Ecology* 80

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Effetti della competizione

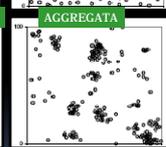
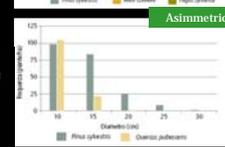
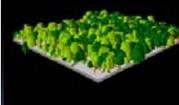
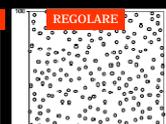
POPOLAZIONE – MEDIO TERMINE:

- Struttura verticale
- Struttura orizzontale
- Struttura delle età
- FUNZIONI del bosco

DINAMICHE DI POPOLAZIONE
Modelli di Lotka-Volterra

39

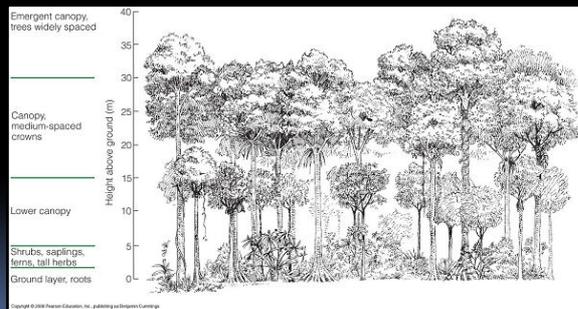
Effetti della competizione



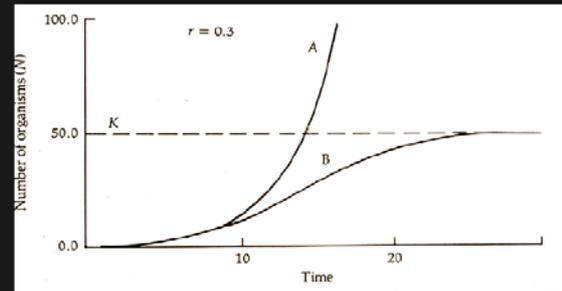
Struttura e tessitura in due pinete di pino silvestre delle Alpi

40

Effetti della competizione



Exponential vs. logistic population growth



Intraspecific (within species) competition: the Verhulst-Pearl Equation

$$\frac{dN}{dt} = rN(K-N)/K$$

- dN/dt is the rate of growth of a species, or the slope of the line.
- In a one species system, the quantity $(K-N)/K$ is the intraspecific competition component because as N approaches K , the change in the population size, dN/dt , approaches 0, but when N is small, dN/dt approaches r , the maximum rate of population increase.
- In other words, individuals of the same species are limiting the population size as the population approaches the carrying capacity.

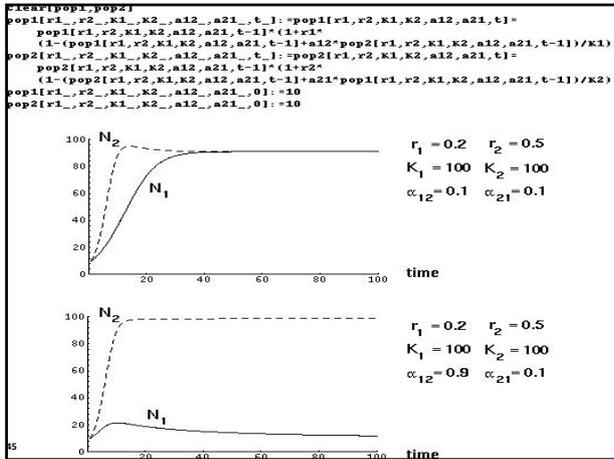
Two species system: Lotka-Volterra equations

- The Lotka-Volterra equations describe the relationship between two species using the same resource.
- Assume a two species system, where the sum of individuals of species 1 and 2 add up to the carrying capacity:

$$N_1 + \alpha N_2 = K_1$$
 where α is competition coefficient for species 2 on species 1, i.e., α is the inhibiting (competitive) effect on species 1 on species 2.
- For a two species system, we can introduce the negative effect of the second species into the Verhulst-Pearl equation by substituting $(K_1 - \alpha N_2)$ for N_1 on the right side of the equation $dN_1/dt = r_1 N_1 (K_1 - N_1) / K_1$.
- For species 1:

$$\frac{dN_1}{dt} = r_1 N_1 (K_1 - N_1 - \alpha N_2) / K_1$$
- For species 2:

$$\frac{dN_2}{dt} = r_2 N_2 (K_2 - N_2 - \beta N_1) / K_2$$
 where β is the competition coefficient for species 1 on species 2.



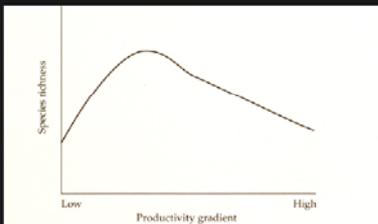
Effetti della competizione

COMUNITA' – LUNGO TERMINE:

- Biodiversità
- Successione
- Rapporti trofici
- Selezione naturale

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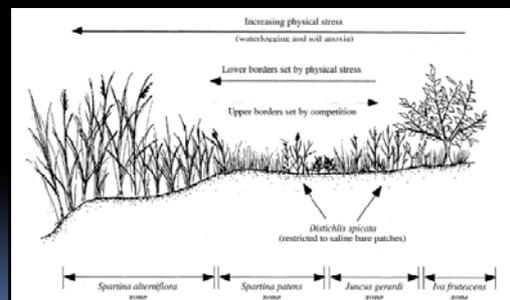
Productivity vs. species richness (Tilman and Pacala 1993)



- Habitats intermediate in resources (and productivity) tend to support the most species.
- Extremely poor soils are likely to be dominated by only a few species that can compete for a single limiting resource.
- Extremely rich soils support high biomass production and are dominated by the few species that compete the most effectively for light.

Effetti della competizione

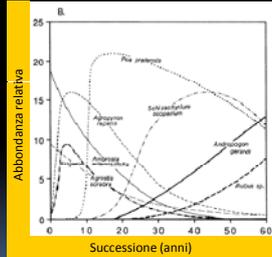
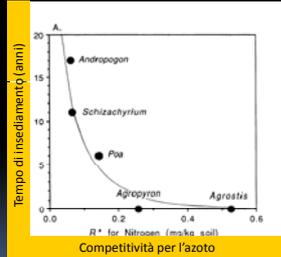
Zonizzazione della vegetazione in paludi salmastre



da Emery et al. (2001), *Ecology* 82

Effetti della competizione

Successione secondaria in campi abbandonati



da Tilman (1994), *Ecology* 75

Effetti della competizione

“Fantasma della competizione passata”

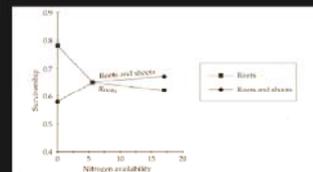


da Franklin et al. (2007), *J.Trop.Ecol.* 23

Resource-ratio hypothesis (Huston and Smith 1987, Tilman 1988)

“Differences in the relative supply rates of limiting resources should lead to differences in the composition of plant communities.”

Models of competition along resource gradients: root vs. shoot competition (Wilson and Tilman 1991)



Wilson & Tilman 1991, cited in Barbour et al. 1998.

Root vs. Shoot competition

Wilson and Tilman examined the survivorship of roots vs. shoots in little bluestem, *Schizachyrium scoparium* along a nutrient gradient.

When N availability was low, root competition was relatively high, and when N availability was high, shoot competition became more important.

Allocation to maintenance: High root-shoot ratios



- Plants in highly stressful environments such as the alpine or arctic often have high root to shoot ratios.

Courtesy of Nival I.TER web site

Plants with high reproductive strategies



- Many annuals and biennials (ruderal species) in weedy environments; produce abundant early germinating seeds; palatable leaves; fast growing; need lots of light; low root to shoot ratios.
- Desert annuals, plants able to take advantage of short moist periods with rapid growth, flowering, and seed set. Can endure long periods of time in dormant state as seeds.

Alliaria petiolata, garlic mustard
www.usgib.edu/~allpet_seedings01_mail.jpg

Papaver escholtzii
http://dpla-map.edcountry.ca.gov/speciesofa_6bio13desert_scribpost.html

Ruolo ecologico

... perché competere?



55

Ruolo ecologico

... perché competere?

Competizione = 

- Sfruttamento risorse
Produttività
- Struttura popolazioni e comunità
- Dinamica Successione
- Selezione nat.
Diversità
Evoluzione

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Ruolo ecologico



Abies balsamea (Thibault et al., 1982)
Araucaria cunninghamia (Bevege, 1968)
Cunninghamia lanceolata (Zhang, 1993)
Picea abies (Gallet, 1994; Pellissier, 1994)
Picea mariana (Mallik and Newton, 1988)
Pinus radiata (Chu-chou, 1978)
 REPLANT PROBLEM (frutteti ed erbacee)

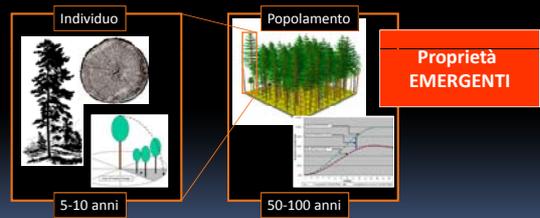
Autoallelopatia: inibisce la rinnovazione di conspecifici.
 Comporta VANTAGGI EVOLUTIVI per la dispersione del seme, la regolazione della densità e distribuzione degli individui, la repulsione di predatori, la riduzione della competizione futura.

da Singh et al. (1999), *Crit.Rev.Plant.Sci.* 18

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L'autodiradamento

Processo gerarchico:
 interazione di livelli spaziali e temporali.



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Autodiradamento

Mortalità da competizione che si verifica progressivamente al crescere degli individui.

Data una certa **capacità portante** esiste un **numero limite** di alberi di una certa dimensione che possono coesistere sulla stessa area.



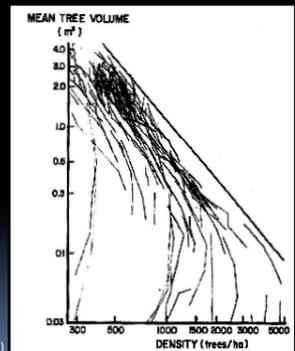
A causa della competizione intraspecifica, **dimensioni massime** degli individui e densità sono inversamente proporzionali.

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Autodiradamento

Popolamenti puri, coetanei, indisturbati.

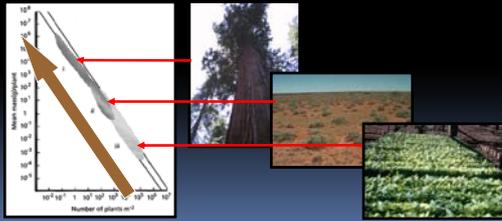
Linea di max densità,
 pendenza = $(-3/2)$.



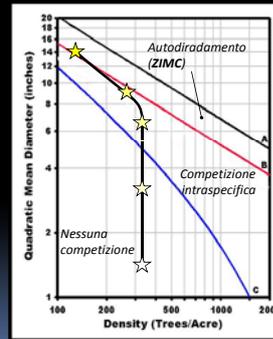
da Drew & Flewelling, (1977, 1979)

Autodiradamento

- Pendenza: costante (??)
- Intercetta: variabile (sciafile > eliofile, conifere > latifoglie)
- Ciascuna specie si dirada lungo una parte della linea globale di autodiradamento.



Autodiradamento



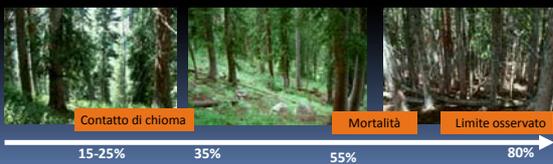
- A. Densità massima e limite dimensionale della specie
- B. Inizio dell'autodiradamento, zona di imminente mortalità da competizione.
- C. Contatto tra le chiome e inizio della competizione.

Significato ecologico

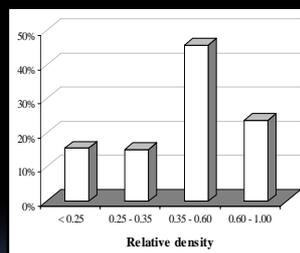
- Limite fisico per lo sviluppo dei popolamenti
- Massimo sfruttamento delle risorse (K)

La vicinanza di un popolamento alla linea di massima densità indica l'intensità della competizione.

Densità / densità massima = DENSITÀ RELATIVA.



Significato ecologico



Densità relativa in pinete di pino silvestre. Popolamenti ancora in crescita attiva dopo le utilizzazioni, competizione << massimo teorico.

Misurare la competizione



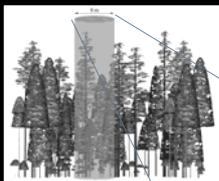
Misurare la competizione



Caratteristiche della risorsa:

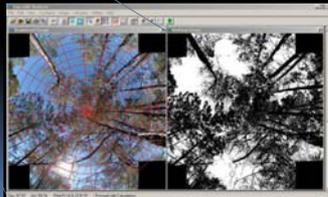
- Disponibilità totale
- "Hot spots"

Misurare la competizione

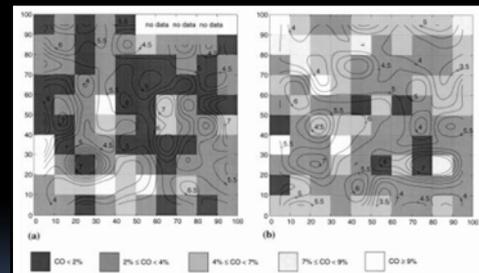


Fotografia emisferica

Luce diretta/diffusa
Canopy openness
Leaf area index
Sunflecks



Misurare la competizione



da Trichon et al. (1998), *Plant Ecology* 37

Canopy openness (grigio) e Plant area Index (isolinee)
in foreste primarie di Sumatra (Indonesia)

Misurare la competizione

Effetti:



Individuo

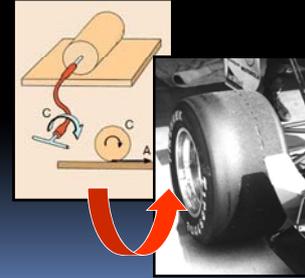
Popolamento

Comunità

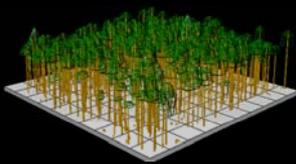
Misurare la competizione

Quantificare gli effetti individuali

- stress
- risposta
- relazione



Misurare la competizione



Numero e dimensione
dei competitori



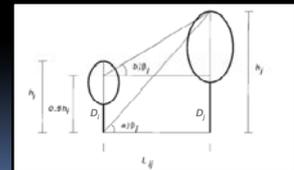
Accrescimento,
sopravvivenza



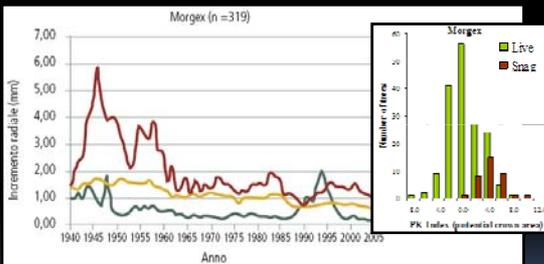
Misurare la competizione

INDICI DI COMPETIZIONE: Basati su numero, dimensioni e
distanza dell'albero soggetto e dei suoi competitori.

Distance-weighted size ratio

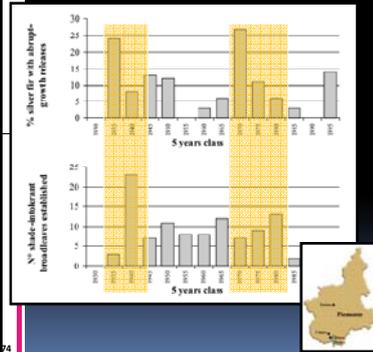


Misurare la competizione



Effetto dei competitori su accrescimento e sopravvivenza di pino silvestre

Misurare la competizione

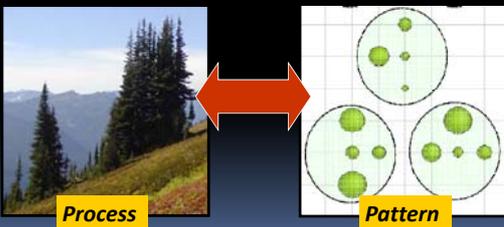


Variazioni repentine di accrescimento in abete bianco e insediamento di specie eliofile in abetine della Valle Pesio

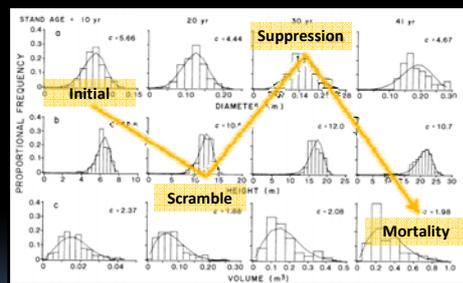
da Motta & Garbarino (2002), *Ann.For.Sci.* 60

Misurare la competizione

Indizi di avvenuta competizione a scala di popolazione:



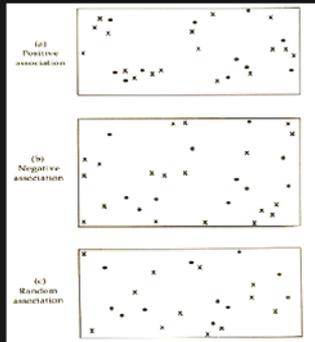
Misurare la competizione



da Knox & Peet (1989), *Ecology* 70

Asimmetria dimensioni ("numero concorrenti in gara")

Using pattern to infer interactions



Positive association: A nonrandom clumped distribution, such as in (a), denotes a positive association between species (e.g., mutualism, or parasitism).

Negative association: If the species show negative association with each other, as in (b), this indicative of a negative spatial association (e.g., allelopathy).

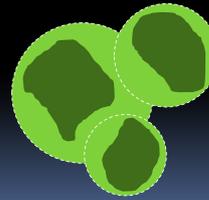
No association: Two species that show totally random dispersal patterns in relation to each other, generally have no interaction, whereas a nonrandom pattern is indicative of an interaction (positive or negative).

• However, these patterns are not necessarily indicative of a relationship. For example, both species may be associated with some environmental factor, such as water availability, and may have no real interaction with each other.

Misurare la competizione

Crown competition factor (CCF)

Rapporto tra area massima di espansione delle chiome (in assenza di competizione) e occupazione reale x 100.



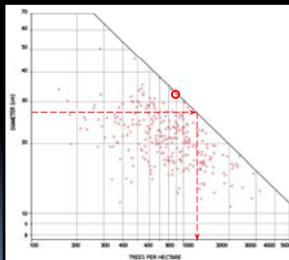
$$CCF(\%) = \frac{\sum_{i=1}^N MCA_i}{\sum_{i=1}^N A_i} \times 100$$

da Krajicek et al. (1961), *For.Sci.* 7

Misurare la competizione

Stand Density Index (SDI)

Densità di fusti da 25 cm che esprime l'affollamento osservato



$$SDI_{sum} = \sum \left[N_i \cdot \left(\frac{D_i}{25} \right)^{1.6} \right]$$

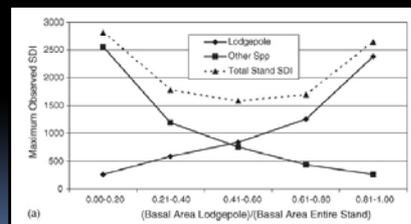


da Reineke (1933)

Misurare la competizione

Stand Density Index (SDI)

- SDI massimo per ogni specie
- Prescrizioni per interventi selvicolturali (USA)



da Woodall et al.(2003), *For.Ecol.Man.* 213

Fischer et al. (2002) Results

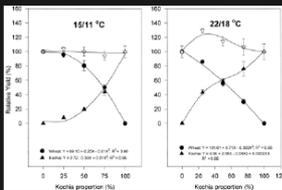
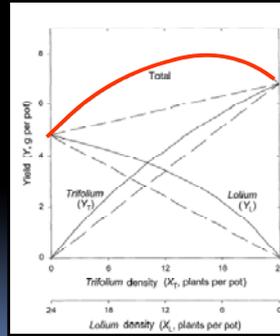


Fig. 2 Relative yields and relative yield totals (RYT) (open triangles) of wheat (solid circles) and kochia (solid triangles) grown at 15/11 and 22/18 °C day/night temperature regimes in replacement-series experiments. Error bars represent \pm standard errors of the mean

- Under high radiation conditions and warm temperatures, growth and photosynthesis were greater for kochia than wheat.
- Warm temperatures also increased dark respiration and reduced water use efficiency under low radiation conditions, however, thus limiting kochia's competitiveness under a closed canopy.
- Water stress did not affect competition.

(Fisher et al. 2000.)

Misurare la competizione

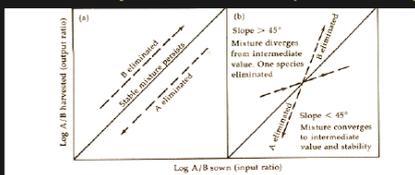


Absolute competition Index (ACI): $Y_L - Y_T$

Relative Competition Index (RCI): $(Y_L - Y_T) / Y_T$

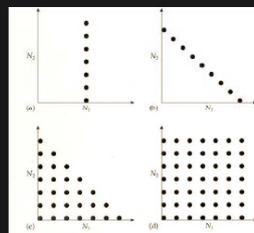
da Jolliffe (2000), J.Ecol. 88

Replacement series (De Wit 1960)



- If the output ratio is equal to the ratio of the input for all seed mixes (diagonal line in (a)) then there is no competition. If for all input ratios, the output ratio (biomass of A/biomass of B) is consistently less than the input ratio (seeds of A/seeds of B) then B will eliminate A, and vice versa.
- If the output ratios vary with differing input ratios, there can be two outcomes.
 - If the slope is $>45^\circ$, then competition will eliminate one of the species depending on the input ratio.
 - If the slope is $<45^\circ$, then there is a stable equilibrium seed ratio.

Other experimental seeding designs for competition experiments



- (a) Partial additive: Can be used to test the effect of varying the abundance of seeds of species 2 against a fixed abundance of seeds of species 1. This tests the effects of species 2 on species 1, but not vice versa.
- (b) Replacement series of DeWit with mixtures varying from total dominance of species 1 to total dominance of species 2. This allows testing the effects on either species on the other.
- (c and d) Additive series are more complex and allow one to test the interaction of a full range of input ratios of seeds.

Competition experiments: Target-neighborhood experiments (Fonteyn and Mahall 1981)



The study site near Cottonwood Springs in Joshua Tree National Park, California. The formation is Colorado Desert on a bajada of the Eagle Mountains, 20 km south of the transition to Mojave Desert. Light grey shrubs in the foreground are the dominant perennial of the system, *Ambrosia dumosa* (Asteraceae).



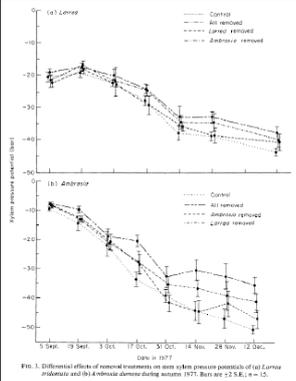
Ambrosia dumosa (Burro weed)
http://www.jepic.org/vol14no1/06JRO

Larrea		Ambrosia	
Control	All removed	Control	All removed
Larrea removed	Ambrosia removed	Ambrosia removed	Larrea removed

- Left: Effect of *Ambrosia dumosa* on *Larrea tridentata* 100 m² plots (clockwise from upper left): (1) control, (2) removing all *Larrea* and all *Ambrosia* except the *Larrea* target, (3) removing all the *Ambrosia*, (4) removing all the *Larrea* except the target.
- Right: Experiment examining control of *Larrea* on *Ambrosia*.
- Examined the effect of the removal experiments on stem xylem pressure of target species.

Fonteyn, P.J. and B.E. Mahall. 1981. An Experimental Analysis of Structure in a Desert Plant Community. *Journal of Ecology* Vol. 69, no. 3, pp. 883-896.

Competition experiments: Target-neighborhood experiments (Fonteyn and Mahall 1981)



(a) *Larrea* showed some reduction in water stress when other plants were removed. This increased somewhat as the summer progressed.

(b) *Ambrosia* showed a much stronger response to removal, particularly of *Larrea*.

Fonteyn and Mahall, 1981.



Gestire la competizione



...e se fosse una foresta di protezione diretta?

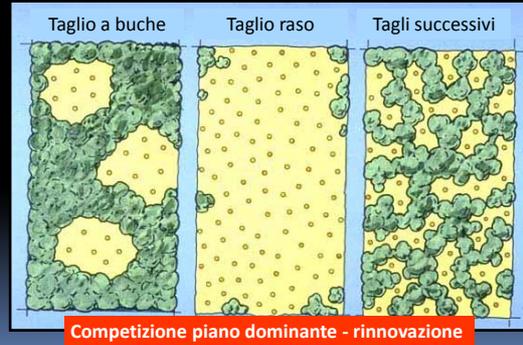
Gestire la competizione

Interventi selvicolturali:

- Alterano i rapporti competitivi
- Riducono la densità
- Concentrano l'accrescimento sugli individui desiderati.



Gestire la competizione



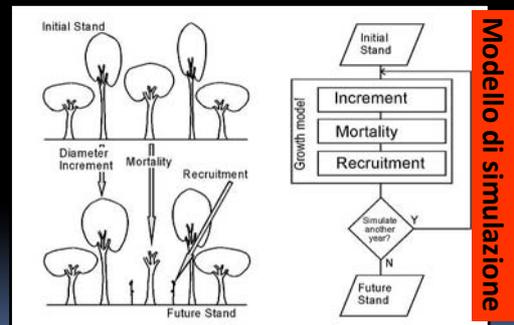
Gestire la competizione



Competizione tra alberi adulti

Prima e dopo un diradamento in *Pinus jeffreyi*, Lassen National Forest, CA.

Prevedere la competizione



da Vanclay (1994)

I prossimi passi

- Letture consigliate (sul sito)
- Casi di studio: osservare & misurare
- Seminario: modelli di simulazione
- Esercitazioni in campo

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Letture consigliate

Antonovics J., Levin D. A. (1980), *The ecological and genetical consequences of density dependent regulation in plants*, Annual Review of Ecology and Systematics, 11: 411-452.

Hutchings M.J., Budd C.S.J. (1981), *Plant competition and its course through time*, BioScience, 3: 640-645.

Long J.N., Dean T., Roberts S. (2004). *Linkages between silviculture and ecology: examination of several important conceptual models*. Forest Ecology and Management 200: 249-261

Long J.N., Smith F.W. (1984), *Relation between size and density in developing stand: a description and possible mechanism*, Forest Ecology And Management, 7: 191-206.

White J., Harper J.L. (1970), *Correlated changes in plant size and number in plant populations*, Journal of Ecology, 58: 467-485.

Tilman D. (1987), *On the Meaning of Competition and the Mechanisms of Competitive Superiority*, Functional Ecology, 1: 304-315.

Zeide B. (1985), *Tolerance and self-tolerance of trees*, Forest Ecology and Management 13: 149-166.

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