

# Tree competition and species coexistence in a warm-temperate old-growth evergreen broad-leaved forest in Japan

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Plant Ecology 164: 235-248, 2002



# Introduction

# 競争モード(competition mode)について

- ・非対称競争(asymmetric competition)

or

主に光競争

一方向的競争(one-sided competition)

→より大きい個体のみが小さい個体に影響を与える  
競争様式

Competition that the only larger plants affect  
the smaller ones

- ・対称競争(symmetric competition)

or

主に地下資源競争

二方向的競争(two-sided competition)

→すべての個体が影響を与える競争様式

Competition that all plants affect

・混んだ単純林の個体間競争は主に光の競争→一方向的競争

competition between plants in crowded monospecific stands may be mainly for light→one-sided or asymmetric competition

(Weiner and Thomas 1986; Hara 1988; Weiner 1990)


・混交天然林での個体成長に基づいた競争と種共生についての研究は少ない

only a few studies on competition and species coexistence based on the growth of individual trees in multi-species natural forest

(Kohyama 1992, 1993; Hara et al. 1995; Kubota and Hara 1995)

→これらの研究は冷温帯林か亜寒帯林での研究

These studies were conducted in cool-temperate or sub-boreal forests.



暖温帯常緑広葉樹林の階層構造は冷温帯林や亜寒帯林より発達→種間競争がより複雑なのでは？

The vertical structure of warm-temperate evergreen broad-leaved forests is more developed than that of cool-temperate or sub-boreal forests, and interspecific relationships between species are assumed to be more complicated.

仮定：暖温帯常緑広葉樹林の林分構造、種構成、種共生と多様度のメカニズムは個体間の競争のモードに強く関係している

We assumed that the stand structure, species composition, and mechanisms of species coexistence and diversity in warm-temperate evergreen broad-leaved forests are strongly related to the mode of competition between individual adult trees.



暖温帯老齡常緑広葉樹林で種内と種間の競争の  
モードに基づいて、個体の成長動態を分析

We analyzed the growth dynamics of individual  
adult trees for the modes of intra- and inter-  
specific competition in a warm-temperate old-  
growth evergreen broad-leaved forest .



# Methods

# Study site

- ・龍良山(対馬)

## The Tatera Forest

(between the Japanese Archipelago and the Korean Peninsula)

- ・標高(altitude):140-190m

- ・常緑広葉樹林(evergreen broad-leaved forest)

スタジイ、イスノキ、ウラジロガシなど

- ・DBH1m以上, H20-30mの個体が優占←老齡林

a general canopy of 20-30m in height dominated trees  
with DBH greater than 1m



# Field measurements

- ・1990年に4ha(200×200m)プロットを設置

4ha plot was set up in 1990

- ・DBH $\geq$ 5cmの個体を対象

woody stems  $\geq$ 5.0cm in DBH were tagged and identified

- ・1990, 1992, 1997年にDBHとx, y座標測定

mapped to the nearest 0.1m as x- and y-coordinates and measured for DBH in 1990, 1992, 1997

- ・樹高は樹冠階層として記録

Tree height was recoded as a vertical canopy layer for each tree according to the crown position.

Layer I : upper canopy layer

Layer II : lower canopy layer and  $\geq$ 8m tall

Layer III :  $<$ 8m tall

# The model and data analysis

- ・1990-1997年の胸高直径成長率(G), 胸高直径成長率のばらつき(D), 死亡率(M) を算出

mean absolute growth rates(G), variance of absolute growth rates(D), mortality rate(M) from 1990 to 1997

- ・プロット内に100個体以上存在する9樹種でモデル解析  
analyze 9 abundant species(>100 individuals per 4 ha study plot)

→イスノキ(*D. racemosum*)、サカキ(*Cleyera japonica*)、ユキツバキ(*Camellia japonica*)、クロキ(*Symplocos lucida*)、スタジイ(*C.cuspidata var. sieboldii*)、ヒサカキ(*Eurya japonica*)、カクレミノ(*Dendropanax trifidus*)、ヤブニツケイ(*Cinnamomum japonica*)、イヌガシ(*Neolitsea aciculata*)

# The model and data analysis

Yokozawa and Hara (1992)

$$G(x,t)=x[a_0-a_1x\ln x-c_1C(t,x)-c_2C(t,x_{\min})]$$

G : 胸高直径成長率(DBH growth rate)

x : DBH

$x_{\min}$  : minimal size in the stand

t : time

$a_0, a_1, c_1, c_2$  : constant

$C(t,x)$  : one-sided or asymmetric competition effect

$C(t,x_{\min})$  : two-sided or symmetric competition effect

# Results



# Size structure in 1990

胸高断面積合計 : 63.5m<sup>2</sup>/ha

total basal area

→スダジイ (*Castanopsis cuspidata* var. *sieboldii*) : 39.3%

イスノキ (*Distylium racemosum*) : 32.2%

立木密度 : 1124/ha

density of stems

→イスノキ (*Distylium racemosum*) : 35.9%

サカキ (*Cleyera japonica*) : 16.8%

ユキツバキ (*Camellia japonica*) : 12.6%

Table 1. The proportion (%) of stems (DBH  $\geq$  5 cm) belonging to each vertical layer of nine abundant species in the 4 ha study plot. Each vertical layer was classified according to crown position and tree height as follows. Layer I: canopy layer; layer II: below canopy and  $\geq$  8 m tall; layer III < 8 m tall.

Species	Species code		Layer		
			I	II	III
Layer-I species					
<i>Castanopsis cuspidata</i> var. <i>sieboldii</i>	CAC	スダジイ	80.7	7.8	11.5
<i>Dendropanax trifidus</i>	DET	カクレミノ	30.1	42.6	27.3
<i>Distylium racemosum</i>	DIR	イスノキ	28.7	31.3	40.0
Layer-II species					
<i>Camellia japonica</i>	CAJ	ユキツバキ	3.0	47.5	49.5
<i>Cleyera japonica</i>	CLJ	サカキ	10.7	37.2	52.1
<i>Cinnamomum japonica</i>	CIJ	ヤブニツケイ	4.2	35.6	60.2
Layer-III species					
<i>Symplocos lucida</i>	SYL	クロキ	4.1	25.6	70.3
<i>Neolitsea aciculata</i>	NEA	イヌガシ	7.1	20.6	72.3
<i>Eurya japonica</i>	EUJ	ヒサカキ	0.0	11.7	88.3

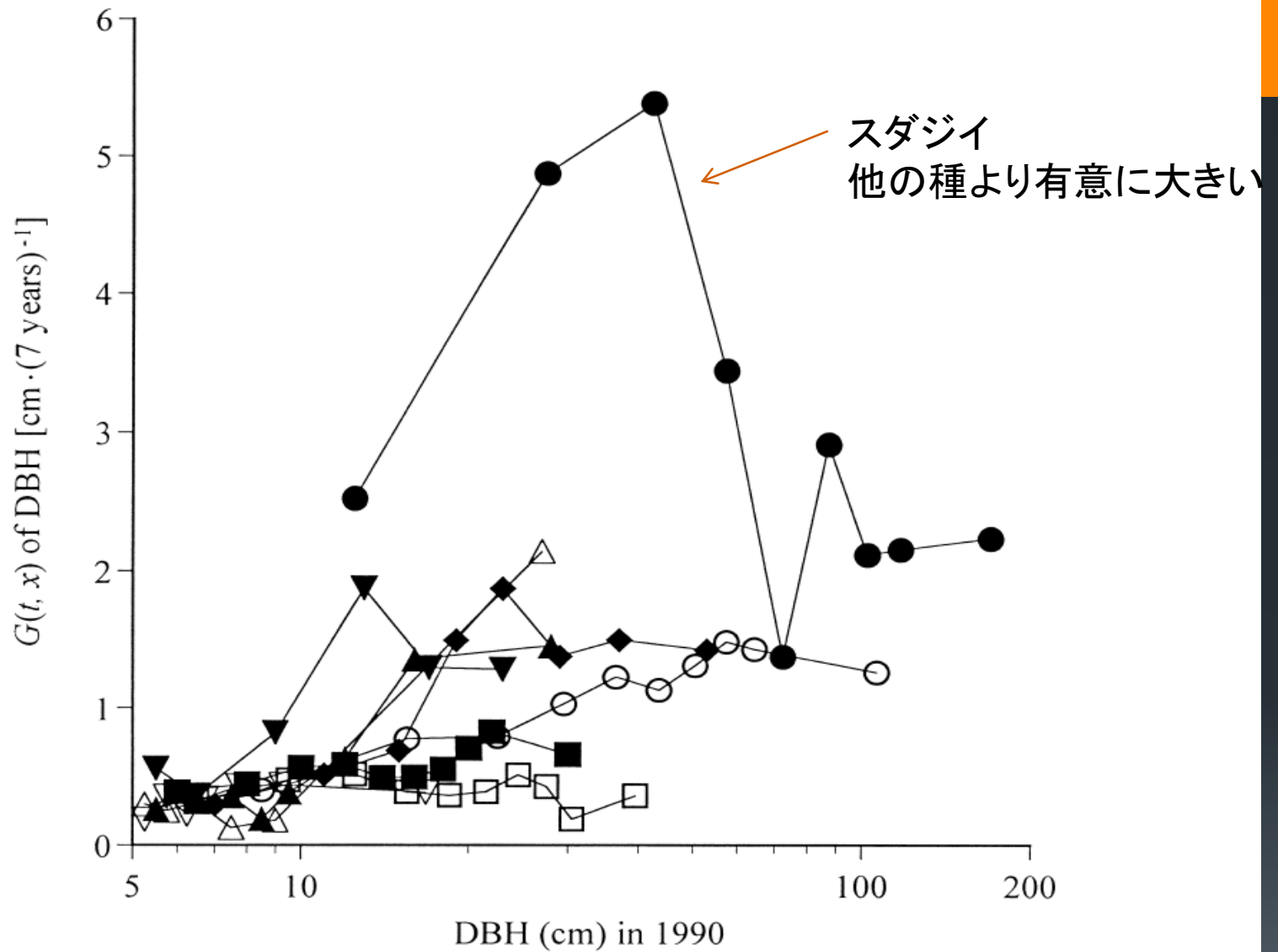


Figure 2. The relationship between DBH in 1990 (log scale) and mean absolute growth rate  $G(t, x)$  of DBH from 1990 to 1997 for nine abundant tree species. ●: *C. cuspidata* var. *sieboldii*, ◆: *D. trifidus*, ○: *D. racemosum*, ■: *Camellia japonica*, □: *Cleyera japonica*, ▼: *Cinnamomum japonica*, △: *N. aciculata*, ▲: *S. lucida*, ▽: *E. japonica*.

「DBH=xの成長率のばらつき」の平方根

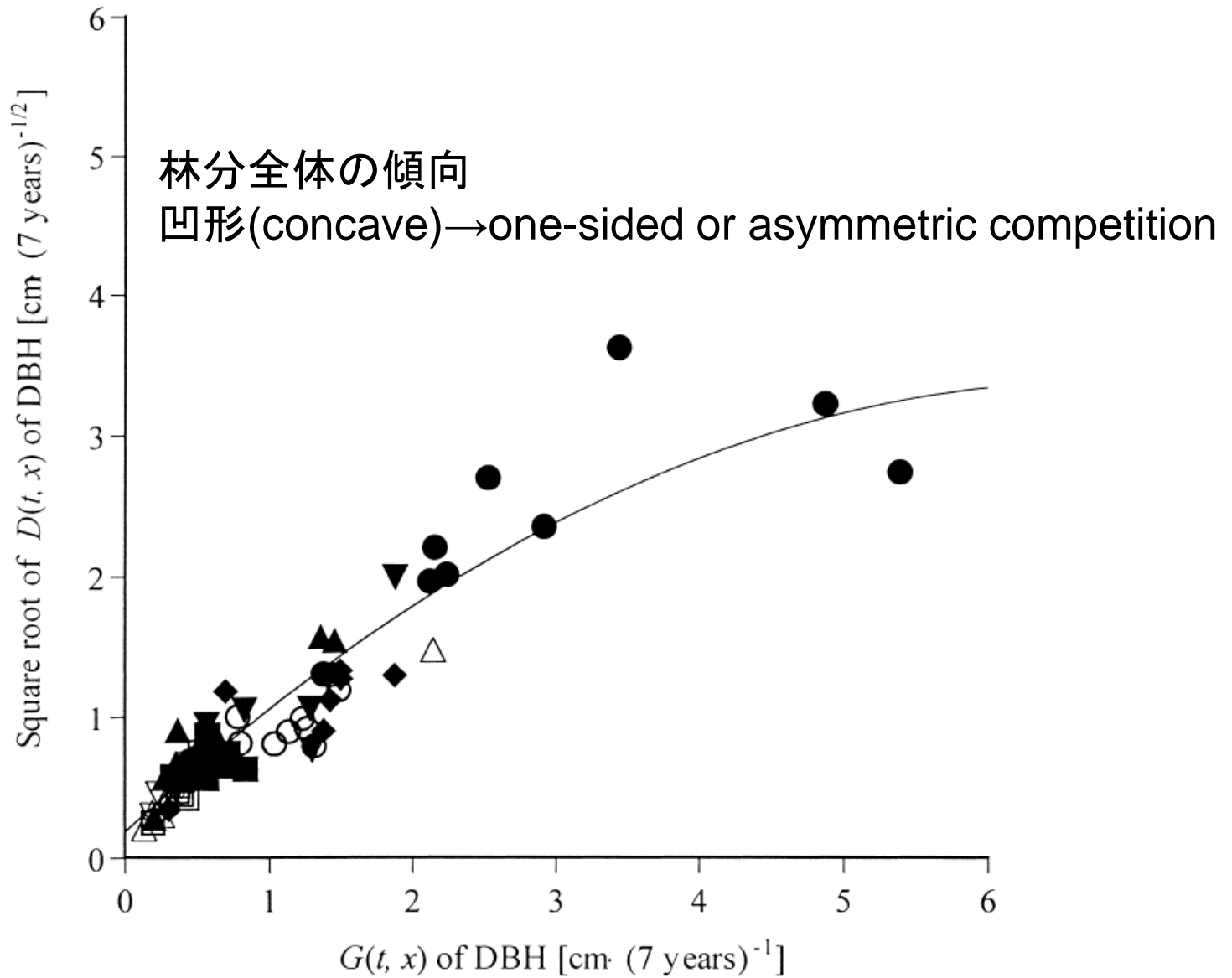
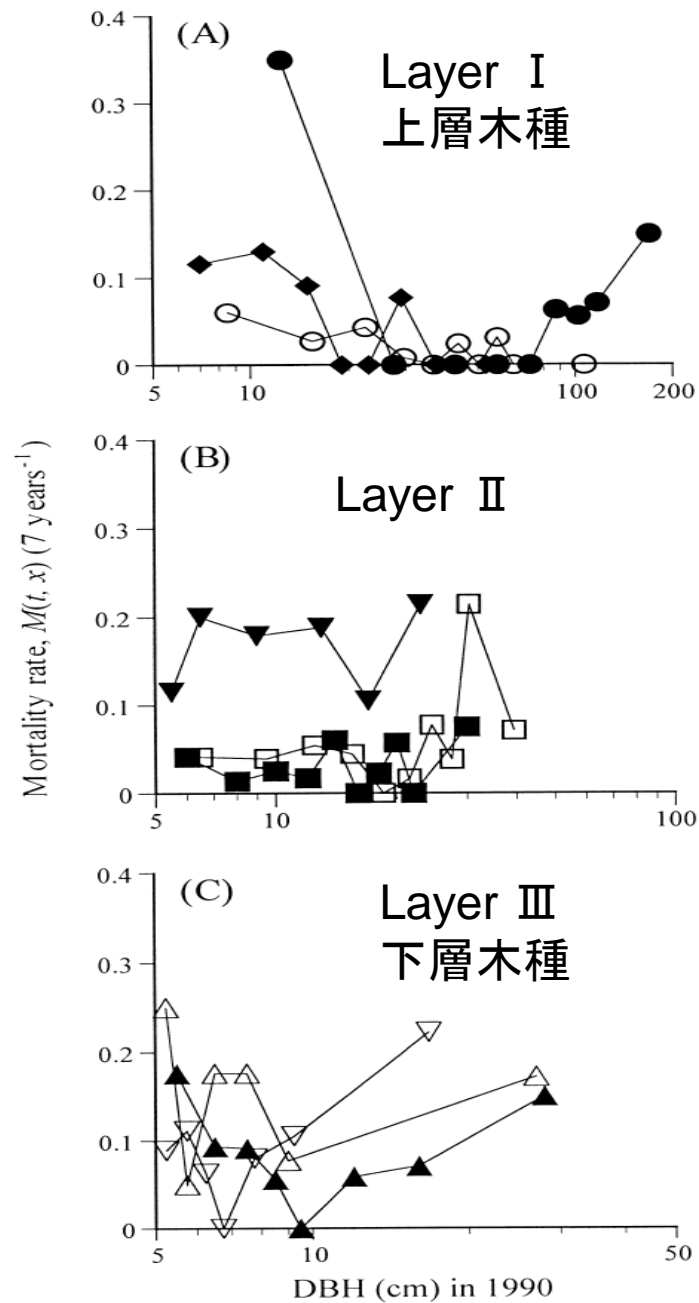


Figure 3. The relationship between mean absolute growth rate  $G(t, x)$  of DBH from 1990 to 1997 and square root of the variance in absolute growth rate  $D(t, x)$  of DBH for nine abundant tree species. Symbols are as in Figure 2.



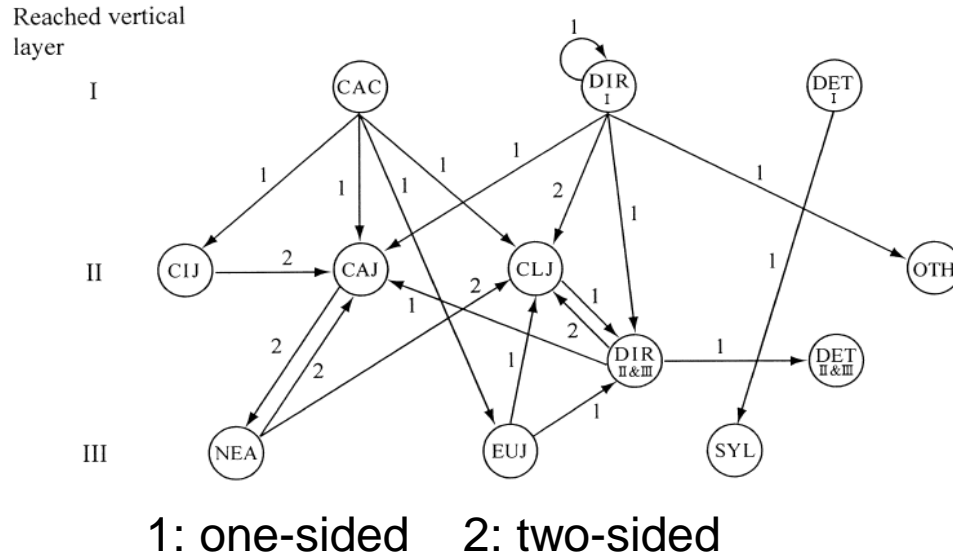
# 死亡率



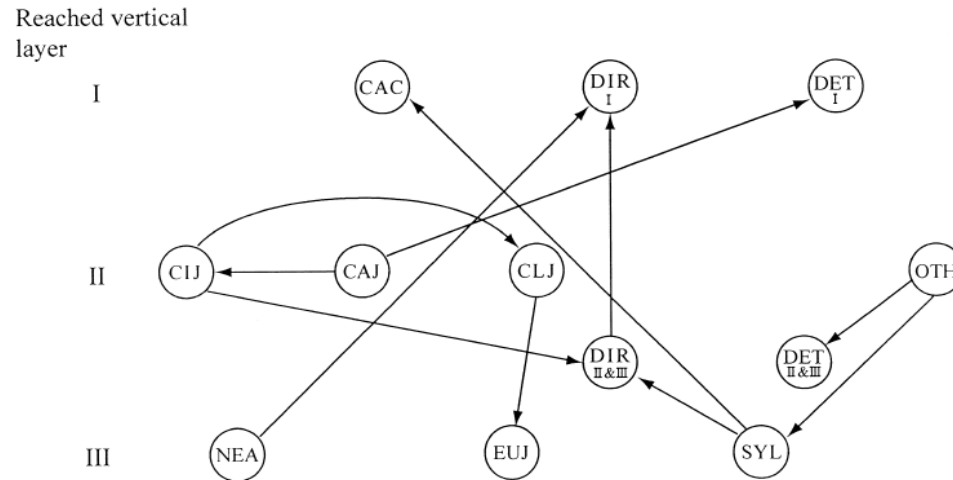
overall  
mortality rate  
per year  
0.97%

Figure 4. The relationship between DBH in 1990 and observed 7-year mortality rates  $M(t, x)$  from 1990 to 1997 for nine abundant tree species. Symbols are as in Figure 2.

(a) Competitive (suppressive) relationship



(b) Positive relationship



CAC	<i>C.cuspidata var. sieboldii</i>	スダジイ
DET	<i>Dendropanax trifidus</i>	カクレミノ
DIR	<i>D. racemosum</i>	イスノキ
CAJ	<i>Camellia japonica</i>	ユキツバキ
CLJ	<i>Cleyera japonica</i>	サカキ
CIJ	<i>Cinnamomum japonica</i>	ヤブニツケイ
SYL	<i>Symplocos lucida</i>	クロキ
NEA	<i>Neolitsea aciculata</i>	イヌガシ
EUJ	<i>Eurya japonica</i>	ヒサカキ

- ・種間競争は主に上層から下層へのone-sided
- ・Layer IIとIII間の種間競争
- ・Layer Iの種は他の種の影響を受けず
- ・同じ層間の競争は少ない

Figure 5. (a) Competitive (suppressive) and (b) positive relationships between trees  $\geq 5$  cm in DBH for the nine abundant species and all the other 26 species. Diagrams are based on the results of multiple linear regression of the theoretical general function form of  $G_k(t, x)$ , Equation (4). In the competitive relationship (a), 'species  $i \rightarrow$  species  $k$ ' represents that species  $i$  suppresses the individual DBH growth of species  $k$  according to Equation (4) [i.e.  $c_{1,i} > 0$  or  $c_{2,i} > 0$  for  $G_k(t, x)$ ]. '1' at the arrow in (a) indicates a one-sided competitive effect (i.e.  $c_{1,i} > 0$  and  $c_{2,i} = 0$  in Equation (4) significant at  $P < 0.05$ ), and '2' at the arrow in (a) indicates a symmetric competitive effect (i.e.  $c_{1,i} = 0$  and  $c_{2,i} > 0$  in Equation (4) significant at  $P < 0.05$ ). In the positive relationship (b), 'species  $i \rightarrow$  species  $k$ ' represents that the individual DBH growth rate of species  $k$  increases with the abundance of species  $i$  [i.e.  $c_{1,i} < 0$  or  $c_{2,i} < 0$  for  $G_k(t, x)$  in Equation (4)]. In (b), all the arrows indicate  $c_{2,i} < 0$  in Equation (4) (significant at  $P < 0.05$ ). See Table 1 for species code. OTH = other species combined.



# Discussion

# Competition between trees of warm-temperate evergreen broad-leaved forest

Layer I : 種特有の生育地をもち、他の種と競争していない  
(upper) species-specific habitat preference  
no competition with other species

Layer II, III : 同じ層間では互いに競争しない傾向  
(lower) II と III 間の二方向的種間競争は地下資源の競争  
正の関係も示す → よく似た生育地を好む  
Layer I から II への一方向的競争は光競争

- no competition with each other in the same layer
- competition between II and III → below-ground competition
- showing positive relationship → similar habitat preferences
- one-sided competition from Layer I to II species  
→ light competition



種間競争は異なる階層間の種共生に重要な役割

Interspecific competition plays an important role  
in the variation in species coexistence between  
different vertical layers.

# Interspecific competition and species coexistence of warm-temperate evergreen broad-leaved forest

- Kohyama(1992, 1995) ← model that consider only one-sided competition

In a warm-temperate rain forest

3種が違う階層で競争・同じ階層の競争は考慮していない

Three major species competed in different vertical layers.

Kohyama didn't consider the competition in the same layers.

- Hara et al.(1995)

In cool-temperate forest

種間競争は少しの種間でしか起きず、正の関係が競争に勝る

Positive interspecific relationship prevailed over competitive relationship.

- Kubota and Hara(1995)

In a sub-boreal forest

種間競争は、統計的には弱く、種共生にあまり関係しない

Interspecific competition don't relate to species coexistence.

今回の結果はKohyama(1992, 1993)を支持

This paper supports Kohoyama's assumption.

- ・異なる階層間の種間競争は一方的競争が多い
- ・同じ階層間では種間競争なし

種多様性の維持機構は暖温帯林と冷温帯林、亜寒帯林では異なる


The maintenance mechanism of species diversity is different between warm-temperate and cool-temperate or sub-boreal forests.

種間競争:冷温帯林や亜寒帯林から暖温帯林の方向に強くなる傾向

正の関係:

//

弱くなる傾向



暖温帯林では、種間競争が冷温帯林や亜寒帯林より複雑で、種多様性もより高い

In warm-temperate forests, interspecific competition are more complex, causing higher species diversity, than in cool-temperate or sub-boreal forests.