

How vegetation-herbivores feedbacks mediate the temperate-boreal forest transition?

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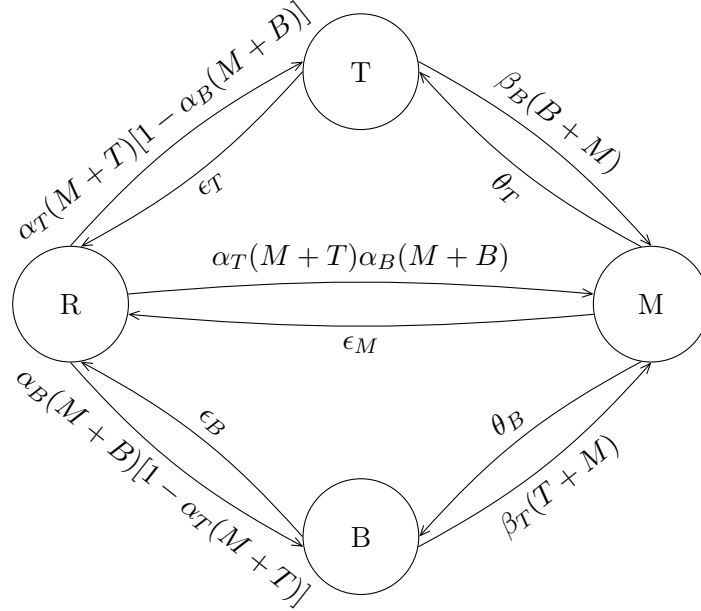
1 Contexte

De nombreux travaux scientifiques attirent l'attention sur les impacts potentiellement conséquents des changements climatiques sur la composition des forêts, et plus particulièrement encore au niveau des écotones. La forêt tempérée devrait migrer vers le nord, à la place de la forêt boréale, où le climat lui sera favorable dans peu de temps. Cependant, d'autres facteurs sont susceptibles de créer un décalage entre le moment où le climat devient favorable et celui où la forêt tempérée va pouvoir s'installer réellement. Parmi les différents facteurs qui peuvent être à l'origine d'un tel décalage, nous pouvons citer la démographie, l'histoire biogéographique et la capacité de dispersion des espèces, les régimes de perturbations (*e.g.*, les feux), ainsi que les interactions biotiques (intra et inter niveaux trophiques).

A l'aide d'une approche de modélisation spatialement implicite, nous nous intéressons ici à caractériser, le long d'un gradient climatique, les équilibres possibles entre la distribution de la végétation (forêt tempérée et boréale) et les populations d'ongulés (cerf de virginie et orignal) en interaction. L'originalité de ce travail est de s'intéresser à la transition entre deux types de forêts, et de prendre en compte l'effet du climat et les interactions trophiques via la relation consommateur-ressource qui traduit à la fois l'impact des ongulés sur la végétation et celui de la végétation sur les ongulés.

2 Model with two forest types

In this case the forest is divided into three types B , T , and M for boreal vs temperate forest, and mixed stands. A fourth state is the regeneration state, post disturbance R .



α_B , α_T are regeneration probabilities (related to seedling survival)
 β_T and β_B are colonisation probabilities
 θ_T and θ_B are competitive exclusion probabilities in mixed forests

Species and states

Boreal: Épinette noire, Épinette blanche, Épinette rouge, Mélèze laricin, Pin gris, Sapin baumier

Temperate: Érable à sucre, Frêne d'Amérique, Frêne noir, Hêtre à grandes feuilles, Ostryer de Virginie, Tilleul d'Amérique, Cerisier tardif

R: Total basal area $< 10\text{m}^2/\text{ha}$

T: A temperate species is present (with $\text{dbh} > 10\text{cm}$) but no boreal species

B: A boreal species is present but no temperate species

M: Both boreal and temperate species are present

N.B. Plots which are exclusively composed of shade intolerant species are removed from the study.

3 Herbivores' dynamics

Based on metaphysiological model (Owen-Smith, 2002).

The herbivore dynamic is modelled as a total **biomass** in the considered landscape.

$$\frac{1}{H} \frac{dH}{dt} = \underbrace{(1 - m)}_{\text{annual survival rate}} \left(\underbrace{cI}_{\text{biomass gains}} - \underbrace{(p + e^{-z c I})}_{\text{biomass losses}} \right) - \underbrace{m}_{\text{mortality by senescence, accidents, hunting...}}$$

When $\text{losses} \geq (1 + \text{gains}) \frac{dH}{dt} = -H$

p is the metabolic attrition rate (per herbivore biomass unit)
 z is a decreasing parameter of mortality rate in function of intake
 m is the minimum mortality rate when food is abundant (senescence, accidents, hunting...)
 c is the conversion between ingested biomass and converted biomass
 I is the vegetation intake rate (consummed biomass per herbivore biomass unit - see next section for details)

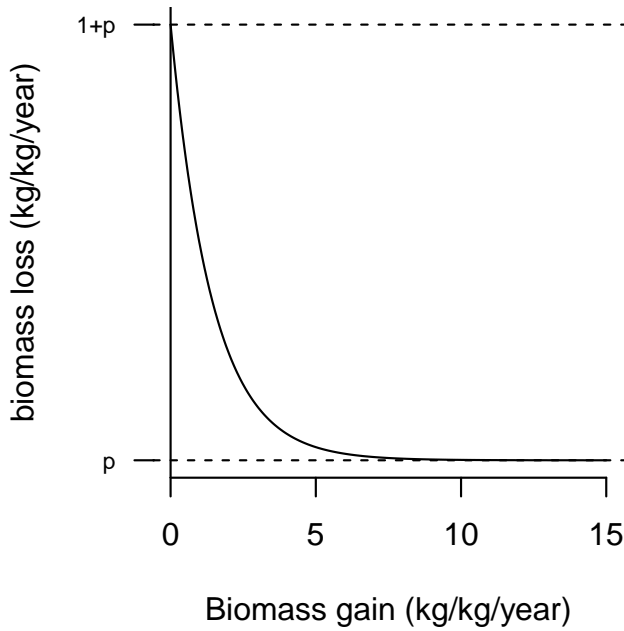


Figure 1: Herbivore mortality depends on the intake. The figure illustrates this relationship for $p = 5.84$; $z = 1$

4 Interactions

4.1 Resources intakes

The intake (biomass consumption per herbivore biomass per time unit) will depend on available resource and the herbivore preferences to have the best quality food. Let's R_1 be the available preferred resource and R_2 the available secondary resource (per herbivore biomass unit). The intake from R_2 will depend on the relationship between the intake from R_1 and $p + m$ (minimum biomass loss rate).

$$I = \overbrace{\frac{\tau F}{\mu + F}}^{\text{intake rate of preferred resource}} + \overbrace{\frac{\rho G}{\nu + G} \left(\phi + \frac{1 - \phi}{1 + e^{r(\frac{\tau F}{\mu + F} - p)}} \right)}^{\text{intake rate of secondary resource}}$$

τ and ρ are the maximum rates of intake (vegetation biomass per herbivore biomass per year) Should be $> p$ for allowing herbivore positive growth.

μ and ν are half saturation parameter for resource intake (available resource for which the intake is half) have to be $\geq \tau$ (τ (or ρ)/(search rate))

ϕ is the coefficient of use of secondary resource when primary resource is abundant. It might be greater than zero in order to depict winter forage and the time spent in forest patches for protection reasons, and consequently a minimum use as a resource too.

r is a smoothing parameter for the switch between use/non-use of the non-preferred resource.

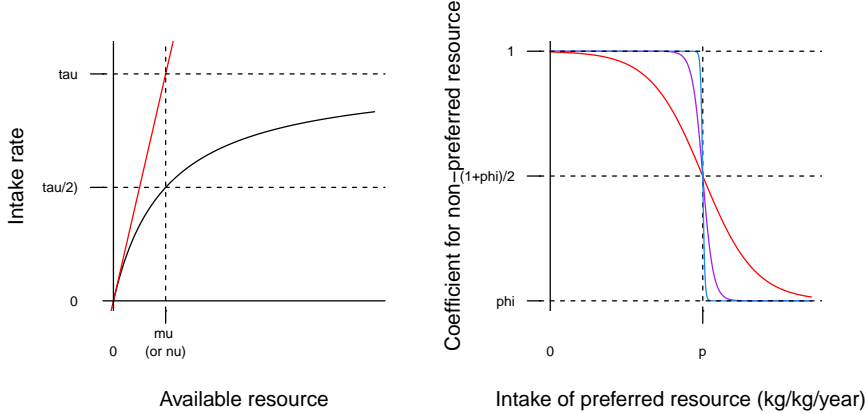


Figure 2: Use of resources. The figure illustrates the mechanisms for $\tau = 10$; $\mu = 10$; $p = 5.84$; $z = 1$; $\phi = 0.8$; $r = 1$ (red); $r = 5$ (purple); $r = 25$ (blue)

Two herbivores: Moose H_a and White-tail deer H_v

Preferred resources

$$F_a = ukR/H_a$$

$$F_v = u(1 - k)R/H_v$$

Secondary resource

$$G_a = (vT + wB + xM)k/H_a$$

$$G_v = (vT + wB + xM)(1 - k)/H_v$$

u , v , w and x are conversions between areas and available biomass (i.e., vegetation density, accessibility), and k is the competitive ability of H_a on H_v .

$$k = e^{-\ln(\frac{1}{k_0})\frac{H_v}{H_a}}$$

In order to match these conditions:

$$\begin{aligned} k &= 1 \text{ if } H_a = 0 \\ k &= 0 \text{ if } H_v = 0 \\ k &= k_0 \text{ if } H_a = H_v \end{aligned}$$

$k_0 = 0.5$ will be used as parcimonious approach. The competitiveness therefore is only varying according to relative biomasses.

Range of variation of total intake I $I_a \in [0; \max(\tau_a k; \tau_a)]$ et $I_v \in [0; \max(\tau_v, \tau_v(1 - k))]$

Shelter effect

The parameter m might be dependent on B (for Moose)

$$m = \frac{m_s}{(1 + (\frac{m_s}{m_0} - 1)B)}$$

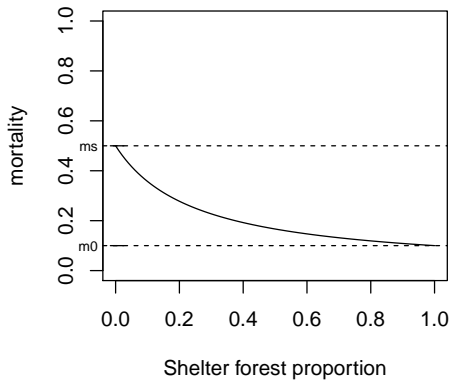


Figure 3: Protective effect of the boreal forest for the moose. m decreases with B . $m_0 = 0.1$; $m_s = 0.5$

m_0 is the mortality (independent from resource) when $B=1$
 m_s is the mortality when $B=0$ (maximum predation and exposition to winds)

5 Herbivores (co)existence

For each herbivore alone, we can compute the biomass at equilibrium ($\frac{dH}{dt} = 0$) for a given landscape (R, T, B, M proportions).

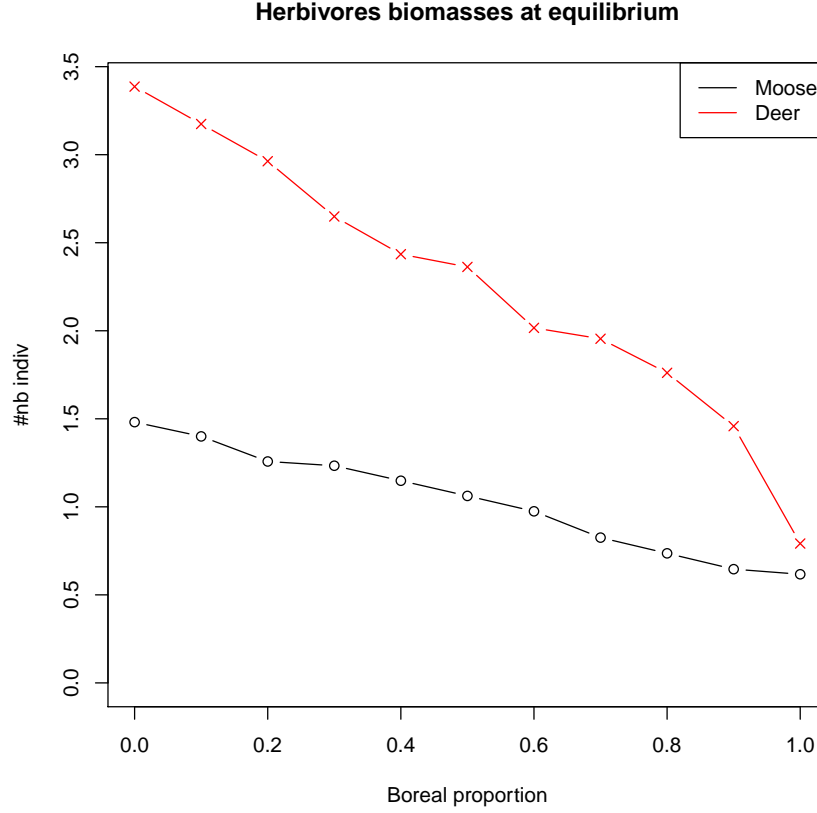


Figure 4: Conditions of existence of the two types of herbivores. The maximum biomass per boreal proportion is represented. In this exemple the parameters are (for 17ha) $u = 17000$; $v=8700$; $w=3400$; $x = 5100$; $p_a = 0.51$; $z_a = 1$; $c_a = 1$; $m_{a_0} = 0.05$; $m_{a_s} = 0.07$; $\tau_a = 5.11$; $\mu_a = 51.1$; $\nu_a = 10.22$; $\phi_a = 0.2$; $r_a = 5$; $p_v = 1.75$; $z_v = 1$; $c_v = 1$; $m_v = 0.2$; $\tau_v = 8.75$; $\mu_v = 87.5$; $\nu_v = 17.5$; $\phi_v = 0.2$; $r_v = 5$

5.1 Feedback effects: impacts on the vegetation

Based on the fact that the impact on demography is as much or more important than the impact on biomass (Moncrieff *et al.* (2014)). The herbivores will affect α , β and ϕ depending on the herbivore pressure on each vegetation state.

Impact on R and α

Per biomass unit intakes for preferred resources (ie R):

$$I_{a1} = \frac{\tau_a F_a}{\mu_a + F_a}$$

$$I_{v1} = \frac{\tau_v F_v}{\mu_v + F_v}$$

We introduce κ , which represents the resource preference (T or B seedlings). $\kappa = 1$ means that the regeneration is null when $P_R = 1$. $\kappa < 1$ limits the herbivore impact when $P_R = 1$.

Impact on R

$$P_{RB} = \frac{H_a I_{a1} \kappa_{B_a} + H_v I_{v1} \kappa_{B_v}}{uR}; P_{RT} = \frac{H_a I_{a1} \kappa_{T_a} + H_v I_{v1} \kappa_{T_v}}{uR}$$

α (α_B , and α_T) decreases from α_0 to 0 proportional to P_R :

$$\alpha_B = \alpha_{B_0}(1 - P_{RB})$$

$$\alpha_T = \alpha_{T_0}(1 - P_{RT})$$

Impact on T, B, M and θ , β

Per biomass unit intakes for secondary resources:

$$I_{a2} = \frac{\rho_a G_a}{\nu_a + G_a} \left(\phi_a + \frac{1 - \phi_a}{1 + e^{r_a(\frac{\tau_a F_a}{\mu_a + F_a} - p_a)}} \right)$$

$$I_{v2} = \frac{\rho_v G_v}{\nu_v + G_v} \left(\phi_v + \frac{1 - \phi_v}{1 + e^{r_v(\frac{\tau_v F_v}{\mu_v + F_v} - p_v)}} \right)$$

Impact on B, T, and M

If ω_T and ω_B represent the relative use of temperate, and boreal (and mixed) forests stands as secondary resources, or the relative time spent there.

The real probabilities of habitat choices (O_T , O_B , and O_M) will also depend on what is available, which means:

$$O_T = \frac{\omega_T T}{\omega_T T + \omega_B B + (1 - \omega_T - \omega_B)M}$$

$$O_B = \frac{\omega_B B}{\omega_T T + \omega_B B + (1 - \omega_T - \omega_B)M}$$

$$O_M = \frac{(1 - \omega_T - \omega_B)M}{\omega_T T + \omega_B B + (1 - \omega_T - \omega_B)M}$$

The final pressures on each seedling type in each forest type ($P_{\text{forest type seedling type}}$) will therefore be (use/availability), accounting for preferences between T and B seedlings (κ):

$$P_{T_B} = \frac{O_{T_a} H_a I_{a2} \kappa_{B_a} + O_{T_v} H_v I_{v2} \kappa_{B_v}}{vT}$$

$$P_{T_T} = \frac{O_{T_a} H_a I_{a2} \kappa_{T_a} + O_{T_v} H_v I_{v2} \kappa_{T_v}}{vT}$$

$$P_{B_B} = \frac{O_{B_a} H_a I_{a2} \kappa_{B_a} + O_{B_v} H_v I_{v2} \kappa_{B_v}}{wB}$$

$$P_{B_T} = \frac{O_{B_a} H_a I_{a2} \kappa_{T_a} + O_{B_v} H_v I_{v2} \kappa_{T_v}}{wB}$$

$$P_{M_B} = \frac{O_{M_a} H_a I_{a2} \kappa_{B_a} + O_{M_v} H_v I_{v2} \kappa_{B_v}}{xM}$$

$$P_{M_T} = \frac{O_{M_a} H_a I_{a2} \kappa_{T_a} + O_{M_v} H_v I_{v2} \kappa_{T_v}}{xM}$$

θ decreases from θ_0 to 0 proportional to P_M :

$$\theta_B = \theta_{B_0}(1 - P_{M_B})$$

$$\theta_T = \theta_{T_0}(1 - P_{M_T})$$

β_B , the colonisation of boreal trees in temperate forest stands is favored by P_{T_T} and decreases if P_{T_B} increases.

$$\beta_B = \frac{1}{2}(1 + \beta_{B_0} \cos(\pi P_{T_B}) + (1 - \beta_{B_0}) \cos(\pi(1 + P_{T_T})))$$

β_T , the colonisation of temperate trees in boreal forest stands is limited by P_B if $\kappa_B < \kappa_T$ and enhanced otherwise

$$\beta_T = \frac{1}{2}(1 + \beta_{T_0} \cos(\pi P_{B_T}) + (1 - \beta_{T_0}) \cos(\pi(1 + P_{B_B})))$$

6 Effects of the environment

Parameter variation along an environmental gradient

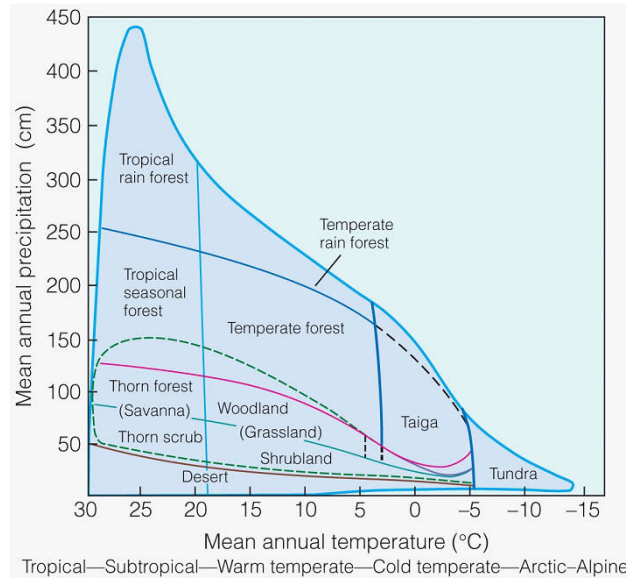


Figure 5: Biomes and climate (left)

Figure 6: Effect of the environment on parameters (right)

From temperate to boreal forest (taiga), precipitation and temperature simultaneously decrease. At the tree line in the Alps or in the Arctic, the change is similar (precipitation and temperature decrease).

The environment will affect the vegetation model (all parameters) but also the available biomasses for the herbivores (u , v , w , x).

The herbivore mortality m (independent from resource) or p (metabolic cost) might also be affected by the environment (eg snow for deer).

7 Parameter list

vegetation model

α_T, α_B (regeneration)

β_T, β_B (colonisation)

θ_T, θ_B (competition)

$\epsilon_T, \epsilon_B, \epsilon_M$ (perturbations)

They will be parametrized using data. We require approximations of **moose and deer abundances in Québec** for all permanent plot locations.

herbivore model, a=moose; v=deer

$z_a = z_v$ (exponential decrease of mortality when intake increases) = 1 (kg/kg) similar to mortality curve in Owen-Smith 2002

$c_a = c_v$ (conversion between vegetation and herbivore biomasses ie food quality) = 0.7 (kg/kg) from Owen-Smith 2002; test $c_a = 0.35$ (digestibility ref) and $c_v = 0.5$

p (metabolic attrition rate) = 5.84 (kg/kg/year) from Owen-Smith 2002 (16g/kg/day) for 200kg. It is the double of the basal metabolic needs. $p_a = 5.84*200/350 = 2.19$??

$p_v = 5.84*200/75 = 10.22$??

N.B. p_v might grow exponentially depending on snow

m_v (minimum mortality rate when resource is abundant) = 0.2 (kg/kg/year) 20% incl. hunting Anticosti ; 0.07 with senescence only from Owen-Smith 2002

m_{a_0} (minimum mortality rate when resource is abundant and $B = 1$) = 0.05 (kg/kg/year) TO REFINE

m_{a_s} (when $B=0$ ie maximum predation and exposition to winds) = 0.07 (kg/kg/year) TO REFINE

τ_a (maximum rates of intake in regeneration patches) = 17? ou 5? (kg/kg/year) TO REFINE ρ_a (maximum rates of intake in mature forests patches)

Un orignal de l'Isle Royale pèse en moyenne 358 kg et consomme 16.7g de feuilles décidues par minute pendant 300 minutes par jour, en moyenne. Donc il mange 5010g / jour * 365 jour = 1 828 650 g / 358 000 g = 5.11 fois son poids (dry mass?)

Second source: 20-25kg/day in summer and 15kg/day in winter on <http://www.hww.ca> fresh mass

τ_v (maximum rates of intake in regeneration patches) = 8.75 (kg/kg/year) from ref 1800g/75kg/day (dry matter content) TO REFINE

ρ_v (maximum rates of intake in mature forests patches)

N.B. In Owen-Smith 2002, $\tau = 14.6$ (kg/kg/year) (40g/kg/day)

$$\mu = \frac{\tau}{\text{search rate}}$$

$$\nu = \frac{\rho}{\text{search rate}}$$

search rate = $\min(1, \frac{\text{travelled area per individual per year}}{\text{study area}})$

Distance per day for moose = 0.86km/day in average over the year = 314km/year

Distance per day from <http://www4.uwsp.edu> 0.78-3.07 km/day (summer) 0.19-1.64 km/day (winter) which gives for deer = 518km/year

For a study area ≤ 17 ha; the search potential is above the size of the study area therefore search rate = 1 and:

$\mu_a = ??$ kg/kg/year

$\nu_a = ??$ kg/kg/year

$\mu_v = ??$ kg/kg/year

$\nu_v = ??$ kg/kg/year

ϕ_a and ϕ_v (% of use of mature forests when regeneration patches give enough resources to feed the minimal needs) = 0.2-0.3 TO REFINE

$r_a = r_v$ (smoothing parameter for the swich between use/non-use of the non- preferred resource) = 5 (FIND UNIT) (then test sensitivity with 1 and 25)

interactions

u, v, w, x (accessible eg <2m high and eatable ressource) (kg/area)

κ_T (preference of temperate tree as resources among all vegetation including herbaceous)

$\kappa_{T_v} = 0.26$; $\kappa_{T_a} = 0.5$

κ_B (preference of temperate tree as resources among all vegetation including herbaceous)

$\kappa_{B_v} = 0.17$; $\kappa_{B_a} = 0.3$

ω_T 0.7; $\omega_B = 0.1$ which depict herbivore (habitats) preferences between (or relative time spent in) the mature forests stands (T, B, M) (here: 70% in T, 10% in B and 20% in M)

8 Coupling both models

Literature Cited

- Moncrieff, G.R., Chamaille-Jammes, S. & Bond, W.J. (2014). Modelling direct and indirect impacts of browser consumption on woody plant growth: moving beyond biomass. *Oikos*, 123, 315–322. URL <http://doi.wiley.com/10.1111/j.1600-0706.2013.00904.x>.
- Owen-Smith, N. (2002). A metaphysiological modelling approach to stability in herbivore–vegetation systems. *Ecological Modelling*, 149, 153–178. URL <http://linkinghub.elsevier.com/retrieve/pii/S030438000100521X>.