EVOLUTION OF LIGHT REQUIREMENT WITH INDIVIDUAL'S SIZE AND LINKS WITH GROWTH PERFORMANCE OF EIGHT-YEAR-OLD BEECH SAPLINGS IN CENTRAL FRANCE

Philippe Balandier*[1,2] , Hervé Sinoquet[1], André Marquier[1] and Marc Vandame[1]

[1] INRA, UMR547 PIAF, F-63100 Clermont-Ferrand, France
Phone + 33 4 73 62 44 39; Fax + 33 4 73 62 44 54; Email philippe.balandier@cemagref.fr
[2] Cemagref, Nogent-sur-Vernisson, France

Introduction

The European beech (*Fagus sylvatica* L.) is a particularly shade tolerant species. For that reason stand regeneration for this species is often considered with the shelterwood system, i.e. keeping a cover of adult trees to steadily supply the stand with seeds, protect young seedlings from adverse climate hazards and avoid a too dense development of understorey vegetation, capable of competition with beech seedlings (Balandier et al. 2006). However if beech can survive to shade, its growth is also considerably limited by light availability. For approximately a decade some results have suggested that light requirements for a significant growth could increase with individual's size rather than with age (Delagrange et al., 2004, 2006; Niinemets, 2006). We tested this assumption for some beech saplings planted in autumn 2000 under the cover of a Scots pine (*Pinus sylvestris* L.) stand thinned to different light intensities in central France.

Materials and Methods

The experiment took place in the Auvergne region of France (45°42′ N, 2°58′ E), characterised by a moderate mountainous climate and relief. In spring 2000 a Scots pine stand was divided in seven plots thinned to achieve different light availability in the understorey ranging in mean from 3 to 98% of incident light above the canopy in the PAR band. These plots were fenced to avoid game predation. In autumn 2000 two-year-old beech seedlings were planted inside them. Stem diameter, height, and crown morphology have been recorded at individual scale since beech plantation whereas light capture, photosynthesis and biomass allocation have been assessed on sub-samples. Transmittance was calculated as the ratio of PAR measured in the understorey at the top of each beech sapling divided by the PAR measured in a close open area during a 24 h period. Links between beech growth or morphological variables and transmittance were analysed by regression at individual scale or by ANOVA with transmittance divided in four classes (table 1).

Results and Discussion

At the plot level the mean diameter growth of beech saplings increased with transmittance (figure 1). The same trend was observed for height growth whereas data were more variable owing to insect damages (data not shown). At individual scale diameter increment on a 3-year period increased with transmittance with a slowing after 0.4 – 0.5 of transmittance but variability, particularly at high light availability (transmittance = 0.98), was important (figure 2). Previous data showed that light actually intercepted by the leaves, i.e. a combination of leaf arrangement and transmittance, gave better results in predicting diameter increment (Balandier et al., 2007).

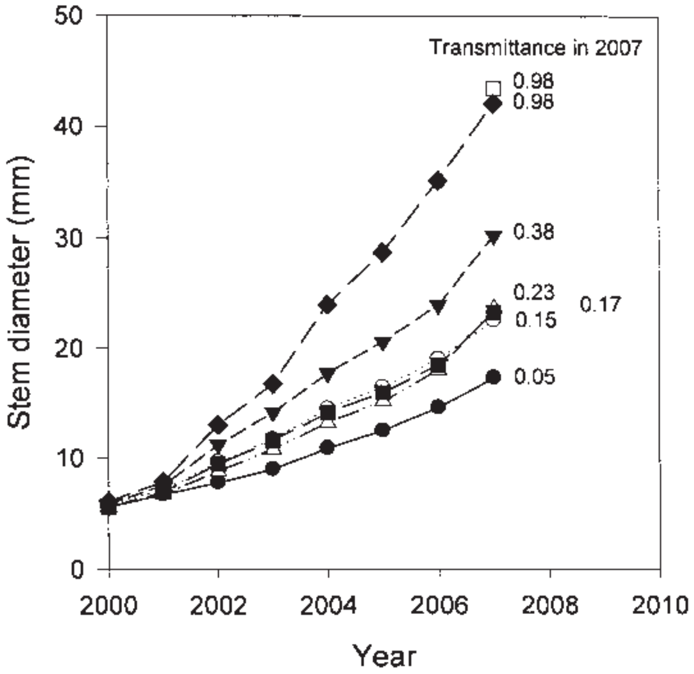


Figure 1: Mean stem basal diameter evolution with year of *Fagus sylvatica* saplings in the understorey of plots of *Pinus sylvestris* thinned to reach different transmittance (PAR in the understorey / incident PAR) values in Central France.

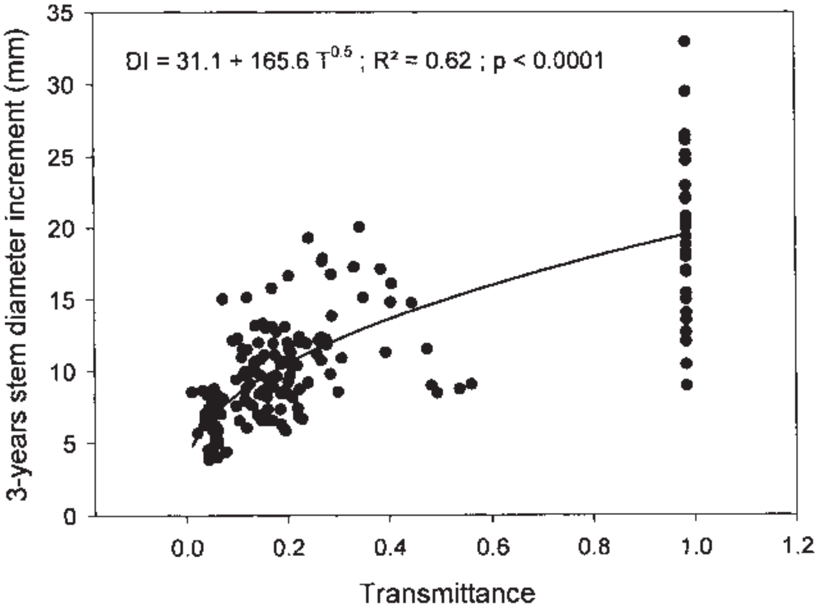


Figure 2: Individual stem basal diameter increment on a 3-year period (2005-2007) of eight-year-old *Fagus sylvatica* saplings as a function of transmittance (PAR in the understorey / incident PAR) in the understorey of *Pinus sylvestris* plots in Central France.

Generally the biomass of the different compartments of the beech saplings increased with transmittance whereas differences were often only statistically different for the highest class of transmittance (table 1). Biomass allocation among the different compartments was statistically not different between the different transmittance classes and the shoot to root ratio was particularly unaffected by transmittance (table 1).

Table 1: Biomass allocation in the different compartments of eight-year-old *Fagus sylvatica* saplings in 2007 according to transmittance classes in the understorey of *Pinus sylvestris* plots in Central France.

Transmittance	Leaf	Root	Shoot	Total	Shoot : Root
0 - 0.10	39 a[#]	55 a	120 a	213 a	2.26 a
0.11 - 0.20	61 a	113 ab	264 a	438 a	2.84 a
0.21 - 0.50	109 a	169 b	407 a	685 a	2.87 a
0.98	395 b	770 c	1341 b	2506 b	2.93 a
p-value	0.0008	0.0001	0.003	0.0009	0.79

[#] Values in a same column are statistically different when followed by different letters (95% LSD test).

By contrast the ratio between total leaf area and total plant biomass (LAR) logarithmically decreased with increasing transmittance (figure 3). The ANOVA between LAR and transmittance was very significant ($p = 0.009$) but this effect almost disappeared when taking into account individual biomass as a covariable in the ANOVA ($p = 0.064$ for transmittance). This can be interpreted as a size effect, the proportion of non-photosynthetic tissues (root, stem) increasing faster than that of photosynthetic tissues (leaf) with individual's size. In addition leaf overlap increased also with beech size reducing accordingly light interception efficiency (Balandier et al., 2007). Therefore light availability to beech sapling should be continuously increased to maintain the same growth rate with increasing individual's size.

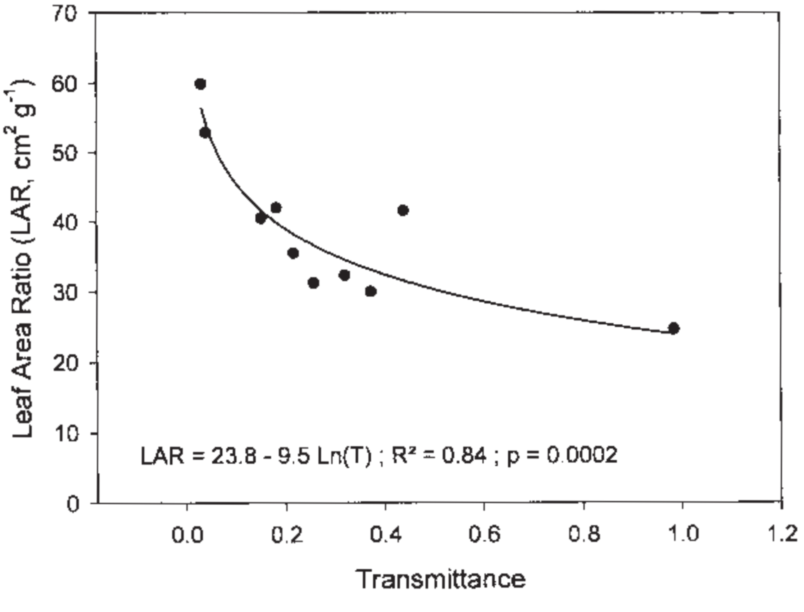


Figure 3: Leaf area ratio (the ratio between total leaf area and total biomass of an individual, $cm^2\ g^{-1}$) of *Fagus sylvatica* saplings in 2007 as a function of transmittance (PAR in the understorey / incident PAR) in the understorey of *Pinus sylvestris* plots in Central France.

References

Balandier, P. et al. 2006. Forestry 79: 3-27.
Balandier, P. et al. 2007. Tree Physiol. 27: 1073-1082.
Delagrange, S. et al. 2004. Tree Physiol. 24: 775–784.
Delagrange, S., et al. 2006. New Phytol. 172: 293–304.
Niinemets, Ü. 2006. J. Ecol. 94: 464–470.

LEAF MORPHOLOGICAL AND FUNCTIONAL ADAPTATION OF SIEBOLD BEECH (*FAGUS CRENATA*) SEEDLINGS GROWN AT TWO WATER REGIMES

Takayoshi Koike*[1,2], Mitsutoshi Kitao[1], Satoshi Kitaoka[3,1] Makoto Watanabe[3,2]
and Yutaka Maruyama[1]

[1] Forestry & Forest Products Research Institute, Hokkaido Research Center
[2] Silviculture and Forest Ecological Studies, Hokkaido University, Sapporo 060-8589, Japan
Tel: +81-11-706-3854 – Fax: +81-11-706-2517 – E-mail: tkoike@for.agr.hokudai.ac.jp
[3] JSPS reasearch fellow at Forestry & Forest Products Research Institute.

Introduction

Siebold beech (*Fagus crenata*) is a dominant tree species in cool temperate zone in Japan and it is characterized by different leaf size and gas exchange rate (Koike and Maruyama 1988) according to the ecological cline (Hagiwara 1977). Individual leaf of *F. crenata* distributed in Pacific Ocean side (PO; xeric) is smaller and thicker than that in Japan Sea side (JS; mesic). The morphological difference is coincided with physiology and mt-DNA variation with ecological cline (Koike et al. 1998, Tomaru et al. 1998). The ecological cline and forest structure may be reflected from the different pattern of precipitation, i.e. summer rain in PO v.s. winter snow in JS (Fujita 1986) as well as natural disturbances by typhoon (Hiura 1996).

This beech flushes leaves in early spring just before snow melt because its vessel is hardly suffered from cavitation maybe due to diffuse porous xylem (Lechowicz 1984). In general *F. crenata* is sencitive to water deficit. However there are differences among origin of beech through Japan (Koike and Maruyama 1998). Do these differences in leaf morphorolgy change in response to soil moisture condition during leaf development?

Leaf thickness and/or leaf mass per area (LMA) of seedlings of oak and magnolia are regulated by the vapor pressure deficit during leaf expansion period (Kitaoka and Koike 2005). Does leaf morphology of *F. crenata* from the contrasting PO and JS have high plasticity according to moisture condition of soil in spring or not? Based on previous studies (Hiura 1998, Koike and Maruyama 1998), it is considered that changes in leaf size and thickness of *F. crenata* in PO may be much smaller than those in JS with dry treatment.

To test this qestion, we examined in beech seedlings of two contrasting populations, PO and JS, raised under dry and wet conditions. Based on these results, leaf anatomical physiology of *F. crenata* is discussed in relation to their natural distribution.

Materials and Methods

The 3 or 4 year-old beech (*Fagus crenata*) seedlings originated from PO and JS were individually planted in clay pot (26 cm in diameter) filled with nursery soil. Nursery soil was Brown forest soil consisting of clay loam slightly mixed with volcanic ash (Koike et al. 2003). Provenance of beech seedlings was Amagi and Fukuoka (from Mt. Seburi) for PO population and Kuromatsunai and Naeba for JS population, and each was belonging to the Forest Office, Forestry Agency Japan. Number of seedlings per one population consisted of 8~12 potted plants. All seedlings were planted for one year under full sunlight prior to the moisture treatment. The experiment was set up at the experimental nursery of Forestry & Forest Products Research Institute in Sapporo. Half of seedlings were wrapped at the bottom part of stem to avoid rain and watered 2 liter per week (Dry treatment). The rest half was kept in nursery and watered 10 liter per week (Wet treatment). The treatments were carried out from late April to early October in 1994. Moisture condition was detected by a soil moisture prove (Daiki, Otsu). Soil moisture of wet and dry treatment ranged between 40~65% and 35% ~40%, respectively.

Gas exchange rate was detected by a porometer (ADC-H4a, Analytical Development Co. Ltd, U.K.). Leaf size (Area meter, AAM5, Hayashi-Denko, Tokyo), leaf thickness (Micrometer, Mitsutoyo, Kawasaki-City), LMA were determined after the determination of gas exchange rate. Water potential of leaf was determined by a Pressure Chamber (SME, California, U.S.A.). The compartment size of leaf was determined under microscope (Olympas, Tokyo) (Terashima 1992) and stomatal density was detected by a SUMP method (Suzuki's Universal Method of Printing, Umemoto-Mori et al. 1998). Leaf nitrogen concentration (N) was determined by a NC analyzer (Yanaco, Kyoto). Chlorophyll (Chl) was analyzed with the DMSO method (Shinano et al. 1996).

Statistical analysis was carried out with two-way analysis of variance (ANOVA) for examining the main effects and interactions of population and watering treatment on all parameters. Mean differences were considered significant at $P < 0.05$. All of the statistical test were performed with R (2.7.0).

Results

Leaf morphological and anatomical traits

There was no statistical difference in leaf traits between the provenances in each population, so that we showed the results of leaf traits only on the population but not provenance. Change in leaf size and thickness of PO was significantly smaller than those of JS ($P<0.01$). Individual leaf size was smaller in the order of PO at wet, PO at dry, JS at wet and JS at dry (Fig. 1). In PO, dry treatment slightly reduced leaf size ($P<0.01$), while dry treartment reduced markedly the leaf area of JS (Fig. 1. left). Although no difference was found in leaf thickness of PO between the moisture conditions, leaf thickness of PO was larger than that of JS. In JS, wet treatment reduced significantly leaf thickness. Overall, there was almost no difference in leaf size and thickness of PO between the moisture conditions.

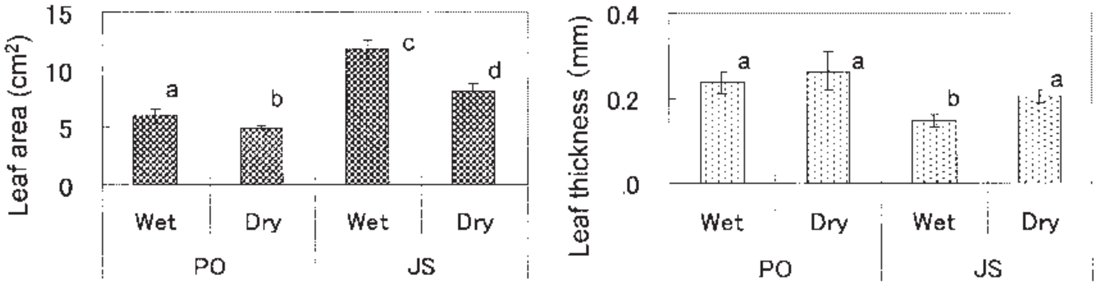


Figure 1: Individual leaf size and leaf thickness of beech seedlings treated with different moisture conditions in nursery. Origin of PO and JS means Pacific Ocean side (i.e. Amagi and Fukuoka) and Japan Sea (East Sea) side (i.e. Kuromatsunai and Naeba), respectively (There was no statistical difference in leaf traits between the provenances in each among one population.) Different alphabet in each figure indicates statistical significance at 5% level.

The compartment size of PO was smaller than that of JS. Among the same provenance, the compartment size was samller with dry condition. Irrespective of populations (PO, JS), the difference in stomatal density of beech leaves was small, however, its beech leaves treated with wet condition was lower than that with dry condition ($P<0.05$). Number of palisade parencyma of PO was two, while that of JS was one. Those were independent of moisture treatments.

Function

Light saturated photosynthetic rate at ambient CO_2 (Psat) of leaves was correlated with leaf thickness. Area based Psat of PO was higher than that of JS at wet condition but there was no difference in dry tratement. Photosynthetic water use efficiency (WUE) was higher in PO than that in JS. An increase in WUE was more increased by dry treatement. There was no difference in the initial slope of light-photosynthesis curves. In fact, leaf Chl. concentration was almost the same among proveances and treatments. Leaf N concentraiton was similar in PO than that of JS. Leaf N concenration of JS with wet tratement was lower than that with dry tratement.

Discussion

Leaf morphology is generally sensitive to environmental stresses (Larcher 2003). We revealed that plasticity of leaf size and thickness of PO was smaller than that of JS. Why does this high plasticity of JS exist? This tendency may be reflected from forest structure and dynamics. Fujita (1986) pointed out *F. crenata* forests in PO mixed with several kinds of species, while those in JS are almost pure stands of beech. It seems that light condition of forest floor of PO is usually lighter than that of JS. Therefore, light condition of JS will change drastically from dark to light in the occasion of disturbance as suggested by Hiura (1996). Beech of JS should acclimate to the rapid change in light and water conditions with high plasticity of leaves.

Psat of PO was higher, which may be attributed to a positive correlation between leaf thickness and Psat (Koike 1988). Thick leaves have more photosynthetic organs per area as found in two layers of palisade parenchyma. Small size of compartment or density of venation of PO and JS with dry tratement is advantageous for avoiding water stress (Larcher 2003). The compartment is formed by the extension of vascular bundle sheath, which prevents transverse movement of CO_2 and vapor in a leaf (Terashima 1992). Therefore, if stomatal regulation is quick and frequent per area, each compartment may be able to avoid water deficit. As a result, WUE may be higher for PO and JS with dry treatment.

In conclusion, large plasticity of JS population may be advantageous for rapid acclimation to sudden changes in light and water conditions caused by disturbances. Even in one species, it is speculated that *F. crenata* may evolve to highly use of water and light condition, especially in JS population. These findings will contribute to reforestation practices in beech forests.

Acknowledgements

Financial support in part by the JSPS Grant-In-Aid are greatly appreciated (Basic Research Type B: 20380083 to Koike, T.). We thank Mr. M.Sanada for NC analysis in beech leaves.

References

Fujita, N. 1986. Plant Sp. Biol. Res. 10: 1-13 (in Japanese).
Hagiwara, S. 1977. Plant Sp. Biol. Res. 1: 39-51 (in Japanese).
Hiura, T. 1995. Oecologia 104: 265-271
Hiura, T. 1998. Trees 12 : 274-280.
Kitaoka, S. Koike, T. 2005. Tree Physiol. 25: 467-475.
Koike 1988. Plant Sp. Biol. 3 : 77-88.
Koike, T. et al. 1998. Acta Bot. 111: 87-91.
Koike, T. Maruyama, Y. 1998. J. Phytogeography Taxonomy 46 : 23-28 (in Japanese).
Koike, T. et al. 2003. Plant Soil 255: 303-310.
Larcher, W. 2003. Physiological Plant Ecology, Springer Verlag, Heiderberg, New York.
Lechowicz, M.J. 1984. Amer. Nat. 124: 821-842.
Shinano, T. et al. 1996. Photosynthetica 32: 409-415
Terashima, I. 1992. Photosyntheis Res. 31: 195-212
Tomaru, N. et al. 1998. Amer. J. Bot. Amer. J. Bot. 85: 629-636.
Umemoto-Mori, M. et al. 1998. Forest Res. Environ. 36: 1-7.

ECOPHYSIOLOGICAL DIFFERENCES BETWEEN NORTH AND SOUTH JAPAN *FAGUS CRENATA* ECOTYPES

Onno Muller*[1], Kouki Hikosaka[2], Ryosuke Nomura[1] and Tsutom Hiura[1]

[1] Tomakomai Research Station, Field Science Center for Northern Biosphere, Hokkaido University, Tomakomai 053-0035, Japan. Tel.+81.144332171
E-mail:onnomuller@hotmail.com
[2] Graduate School of Life Sciences, Tohoku University, Aoba, Sendai 980-8578, Japan

Introduction

Temperature is one the determinants for leaf characteristics of ecotypes distributed over a latitudinal range. With rising global temperatures the interest in identifying and evaluating leaf traits that determine plant's photosynthesis and distribution increases. In this study we evaluate the leaf traits of ecotypes of *Fagus crenata* distributed from south to north Japan.

Along a latitudinal range also other environmental factors interact with temperature that can affect the leaf traits as well as plant's distribution. For *Fagus crenata* in Japan the current distribution can be predicted by a combination of temperature and precipitation variables (e.g. Matsui *et al.* 2004) whereas for its northern limit summer precipitation is shown most influential (Yagihashi *et al.* 2007).

It has been recognized for long in *Fagus crenata* in Japan that there is a geographic cline in which leaf size gradually increases from south-western to north eastern populations (Hagiwara 1977). This might be explained by the optimal leaf size theory for photosynthesis under a light moisture gradient (e.g. Parkhurst and Loucks 1972). Subsequently the importance of leaf size on shoot dynamics and architecture was shown (Hiura 1998) and that the mass base photosynthetic capacity did not differ between populations (Koike et al. 1990).

However a study on the ecophysiological important photosynthesis nitrogen relationship was lacking until now. Therefore we question how the photosynthetic capacity, nitrogen content and the photosynthetic nitrogen use efficiency differ between ecotypes of different latitude and its adaptation to several environmental factors.

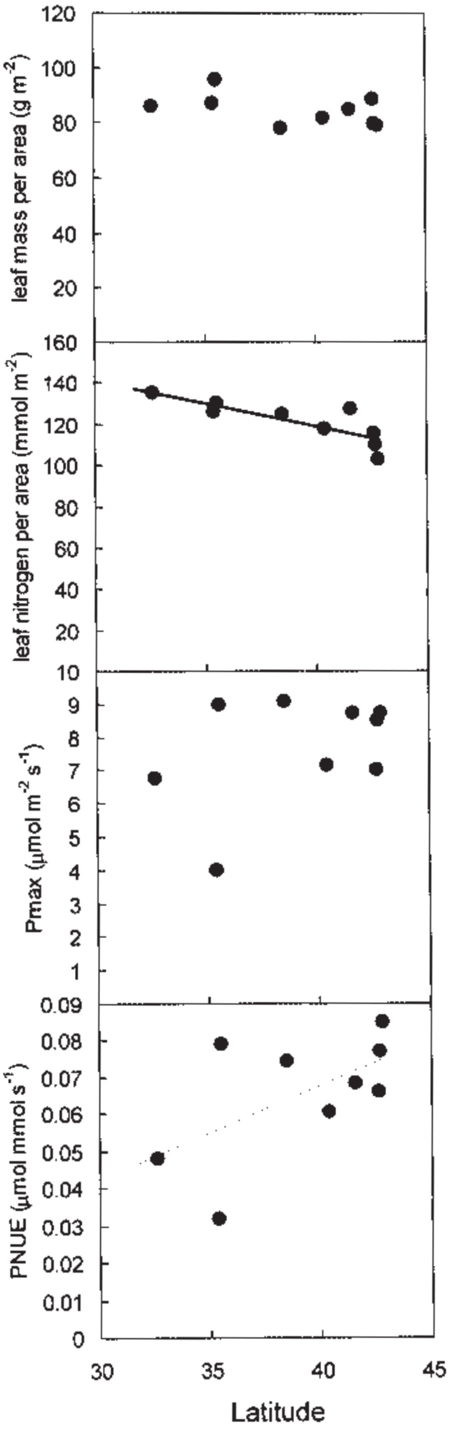


Figure 1: The means of 2-3 trees per provenance of leaf mass per area, nitrogen per area, photosynthetic capacity (Pmax) and photosynthetic nitrogen use efficiency (PNUE) grown in a common garden in Hokkaido in June 2008. Significant linear regression line is shown for nitrogen ($y=-2.25x+209.36$, $r^2=0.68$, $p=0.006$) and for PNUE marginal significant ($y=0.0026x-0.035$, $r^2=0.35$, $p=0.096$)

Materials and Methods

Fagus crenata from 9 provenances from south to north Japan were grown in a common garden in Tomakomai Experimental Forest, Tomakomai, Hokkaido, Japan. Of the about 20 year old trees we determined in June 2008 the photosynthetic capacity at saturated light and a CO_2 concentration of 380 ppm of 3-4 fully exposed leaves per tree and 2-3 trees per provenance. Preliminary the leaf mass per area and leaf nitrogen content were determined of a subset of 4 leaves per tree. For at least 2 trees of the Hokkaido (north, large leaves) and Kyushu (south, small leaves) rainfall was cut from about 2 m around the stem (rain cut treatment), leaves of complete tree were cut into half (herbivory treatment) in spring 2007 two weeks after full expansion of the leaves and leaf characteristics were determined of the remaining half of the leaf and a combination of both (raincut + herbivory treatment) and a control treatment, we determined in August 2007 preliminary the same parameters as we determined for all provenances. Statistical analyses were done using SYSTAT (Systat software Inc. San Jose).

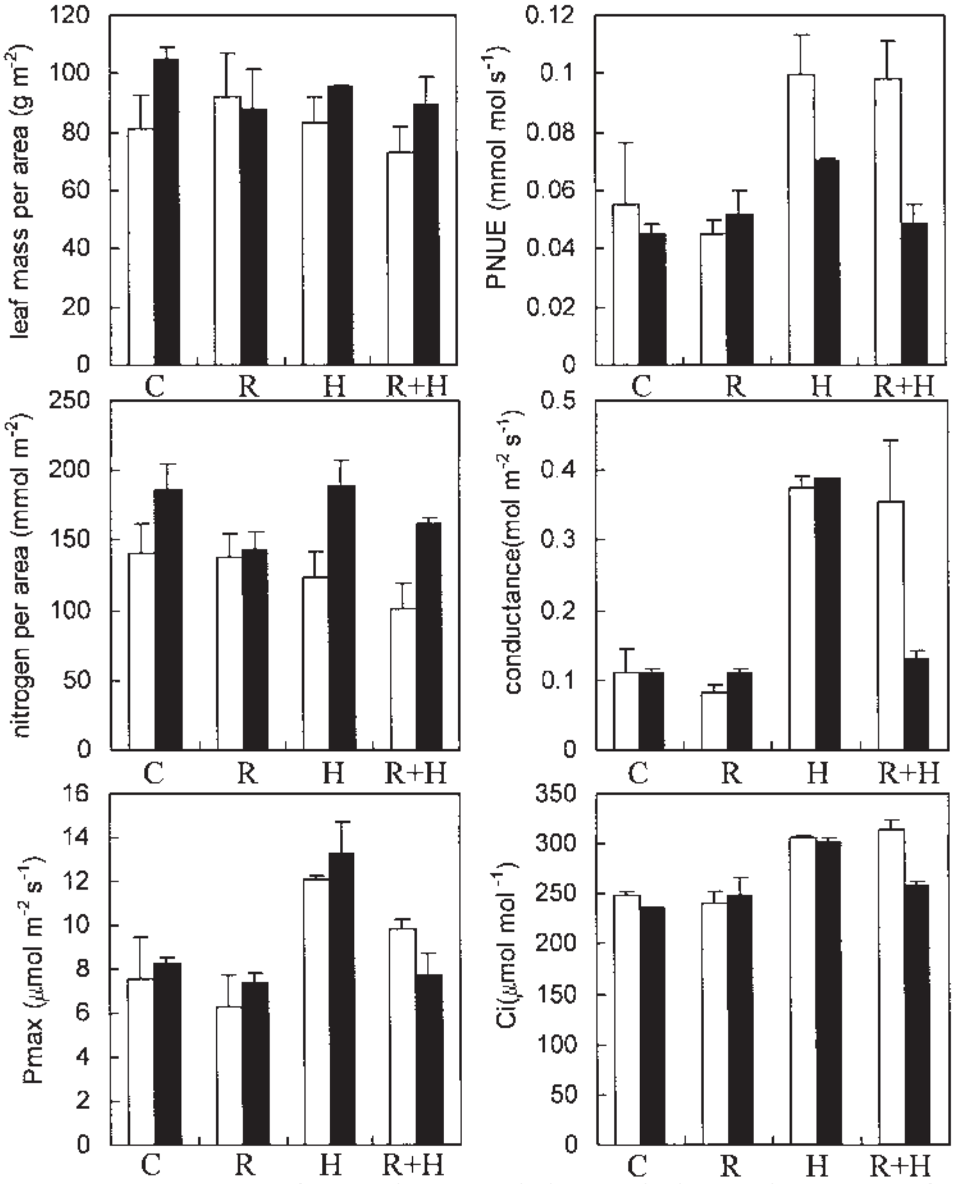


Figure 2: The means for leaf mass, nitrogen and photosynthetic capacity per area, photosynthetic nitrogen use efficiency, leaf conductance and intercellular CO_2 concentration (Ci) of trees of the northern provenance (open bars) and southern provenance (closed bars) (n=2 ± SD) grown in Tomakomai Hokkaido in August 2007 with no treatment (control, C), rain shielded 2 meters around the stem (rain-cut, R), leaves of complete trees cut into half (herbivory, H) and a combination of herbivory and raincut (H+R)

Results and Discussion

The leaf mass per area did not significantly change with latitude (fig.1) although the geographical cline in leaf size (Hagiwara 1977) remained for the trees grown in the common garden (data not shown). The observation that larger leaves are thinner and have greater air space ratio that results in a lower Pmax in *Fagus crenata* (Koike *et al.* 1990) thus doesn't necessary have to be the case in this study. Correspondingly there was no clear latitudinal pattern in Pmax (fig. 1).

However the leaf nitrogen content decreased with latitude and consequently the photosynthetic nitrogen use efficiency tended to increase with latitude (fig 1). This can be explained by a trade off in allocation of nitrogen between photosynthesis and structure (Hikosaka 2004). Onoda et al. 2004 showed that for plants with a later germination time the relative investment in photosynthesis increased. Similarly the *Fagus crenata* from southern population might be adapted to an early germination and longer leaf life span than the northern population. As such they might be exposed to a higher herbivory rate during their life time than northern populations and benefit from relative large investment in structural nitrogen.

In the comparison between north and southern population grown in the common garden in Tomakomai in 2007 the results differed a bit from the general latitudinal trend. The leaf mass per area was larger for the southern than the northern population and so was the leaf nitrogen content and Pmax (fig. 2). This pattern in all except for the rain-cut treatment however did not differ from the observed latitudinal trend of a lower PNUE in the southern population (fig. 2).

The rain-cut treatment had a negative effect on the leaf mass, nitrogen per area and Pmax in the southern population but a slightly positive effect in the northern population resulting in no difference between the populations in this treatment and a slightly higher PNUE after rain-cut for the southern population. This weakly supports the optimal leaf size theory (see intro). However in combination with herbivory and rain-cut small leaves did not perform better than large leaves. In which the PNUE decreased, in part, as a result of the reduced Ci due to limited conductance (fig. 2).

Herbivory resulted in an increase in leaf nitrogen content in southern populations and slight decrease in northern populations without clear changes in leaf mass per area and Pmax. Consequently the PNUE in the northern populations increased largely with herbivory but only slightly in southern populations. Thus the similar pattern among latitudes is emphasized by a simulated herbivory attack. After the attack it might be that leaves of southern populations invest more nitrogen in leaf structure whereas northern populations choose to reallocate their leaf nitrogen to other sources.

In conclusion the preliminary data in this extended abstract show that there is a decrease in leaf nitrogen content and increase in PNUE with latitude that might be influenced by the herbivore pressure experienced in southern populations. Further study will, among others, evaluate the year after effect of a simulated herbivore attack on the several leaf traits.

References

Hagiwara S. 1977.Shuseibutsuaku-kenkyu 1:39-51
Hikosaka K. 2004.J Plant Res 117: 481-494
Hiura T. 1998. Trees. 12: 274-280
Koike T *et al.* 1990.Trans Hokkaido Br Jpn For Soc 38: 20-22
Matsui T. *et al.* 2004. J Veg Sci 15: 57-66
Onoda Y. *et al.* 2004. Funct Ecol 18: 419-425
Parkhurst D.F. and Loucks O.L. 1972. J Ecol 60:505-537
Yagihashi T. *et al.* 2007. Plant Species Biology 22: 217-225

MODELLING LONG-TERM NUTRIENT SUSTAINABILITY OF SWEDISH BEECH FORESTS

Ingrid Stjernquist*[1], Peter Schlyter[1] and Kerstin Sonesson[2]

[1] Dept. of Physical Geography and Quaternary Geology, Stockholm University,
SE-106 91, Stockholm, Sweden, Tel: +46733822272 - Fax: +46 8 164794 - E-mail:
ingrid.stjernquist@natgeo.su.se
[2] Dept of Nature, Environment and Society, Malmö University, Sweden

Introduction

A future sustainable forest management in Sweden under climate change most likely will have to accommodate a change in tree composition from the current situation where conifers are dominating, in particular Norway spruce (*Picea abies*), to a situation with a higher percentage of deciduous species, either in monocultures or in mixed stands (Koca et al. 2006, Löf 2006). Beech (*Fagus silvatica*) is one of the major tree species that, under a milder climate, will increase its natural range towards to the north (Koca et al 2006). Today, concentrated in the southern and coastal parts of Sweden, beech stands are growing on soils ranging from haplic podsols to eutric cambisols. The forests have, for over four decades, been affected by high acid and nitrogen deposition, which have caused nutrient imbalances and decreased tree vitality. The soil nutrient pool has decreased even on highly productive cambisols (Braun et al. 2005, Stjernquist et al 2002). As a concept, sustainability can be defined from several perspectives. However, for a forest ecosystem a sound nutrient balance is fundamental and determines the long-term production as well as the structure and functions of the ecosystem. Forest management may be regarded as geochemically sustainable when the of nutrient loss through leaching and biomass removal is balanced by nutrient inputs through weathering and deposition. Therefore, long-term nutrient balance under current air pollution deposition and climate change is crucial for future beech stand growth and vitality. The objective of the study is to 1) analyze the relationship between deposition of nitrogen and acid compounds, changes in soil chemistry and vitality of beech and mixed beech-oak stands and 2) To evaluate if the current deposition and forest management will be long-term sustainable under climate change.

Material and Methods

The beech and mixed beech/oak (*Quercus robur*) stands used in the study were taken from the beech and oak database of the Swedish National Board of Forestry. The database was originally set up in 1988 for monitoring of forest condition. For each stand, the database includes tree age, height and stem diameter as well as soil chemistry. The stands are growing on podsols (25%) and cambisols (25%) and podsolized cambisols (50%). The soils are acidified with a pH below 4,2 for 90% of the stands.

The model

Conceptually the nutrient balance may be calculated as:

$$\text{Deposition} + \text{Weathering} = \text{Harvesting} - \text{Leaching}$$

Deposition adds acid compounds, nitrogen and base cations to the forest stand. Weathering and leaching processes, as well as the nutrient uptake by the trees are all affected by the deposition. The weathering adds base cations (Na, Ca, Mg, K) to the soil profile and is calculated through the kinetic relationships between the most important minerals. Nutrient loss through biomass harvesting is determined by the nutrient concentration in the stem and the yearly stem growth. The soil processes, the water input through precipitation and the water uptake by the tree, determine the chemical composition of the water leaching from the soil profile.

The deposition is calculated with a regional MATCH model, a dispersion model with a 5x5 km grid, which is more detailed compared to the MATCH model for Sweden (Langner et al. 2000). The weathering rates were calculated using the steady-state biogeochemical model PROFILE (Warfvinge and Sverdrup 1992, 1995). The main factors affecting the weathering are soil mineralogy, soil moisture, and soil texture. The size of the soil volume from which weathering is included in the mass balance is determined by the effective rooting depth, defined as the horizon where 90% of the fine roots are found. The rooting depth is decided by the base saturation in the 20-30 cm depth soil layer. The growth functions for beech and oak are developed for Swedish conditions (Hagberg and Matern 1975).

A number of coupled GCMs (HadAM3H, ECHAM4/OPYC3 and ECHAM5/MPI-OM) and RCMs (RCA3 and RCAO) have been used to assess future climate change in Sweden (see SMHI 2007). Model output show increased yearly mean temperatures for our study area; for the period 2071–2100 in the range of 3–5°C, a change in mean yearly precipitation of 40–50 mm/yr, with the latter value predominating the runs, and for most runs a change in mean yearly run-off of 50mm, though out-put show one scenario run with a decrease of 40 mm/yr. We have used an increase in mean yearly temperature of 5°C, in precipitation of 50mm/yr and of run-off of 50 mm/yr in our calculations to assess climate change impact on nutrients sustainability.

Results and Discussion

The PROFILE modelling give the critical load of acidity or nitrogen for each stand. The critical load is defined as the amount of acidifying compounds, or deposited nitrogen, which will have no long-term negative effects on the forest ecosystem. Exceedance signifies that the current deposition and forest management cause a negative nutrient balance.

Beech: The dominating part of the Swedish beech stands has a critical load for the deposition of acid compounds between 50-100 mmol$_c$ m^{-2} yr^{-1} and a critical load for nitrogen between 73-128 mmol$_c$ m^{-2} yr^{-1}. For 80% of the stands the critical load for acid compounds is exceeded, i.e. showing a value above 0 (Fig 1a). This indicates that, in spite of decreasing deposition of acid compounds over the last years, beech stands growing on leached cambisols as well as on podsols cannot buffer the current deposition input. With current management, beech forests have a lower yearly growth compared to the intensive managed and more economical important spruce forests. In the PROFILE model the nutrient uptake through growth was calculated for a yearly growth of 4-5,5 m^3, i.e. half of the spruce production on the same kind of soils (Sverdrup et al 2005). A higher demand for biomass output would increase the nutrient loss from the ecosystems and further decrease their long-term sustainability. For none of the beech stands were the critical load for nitrogen significantly exceeded, however, all stands have values close to zero, indicating that the beech forests are sensitive to environmental and management changes.

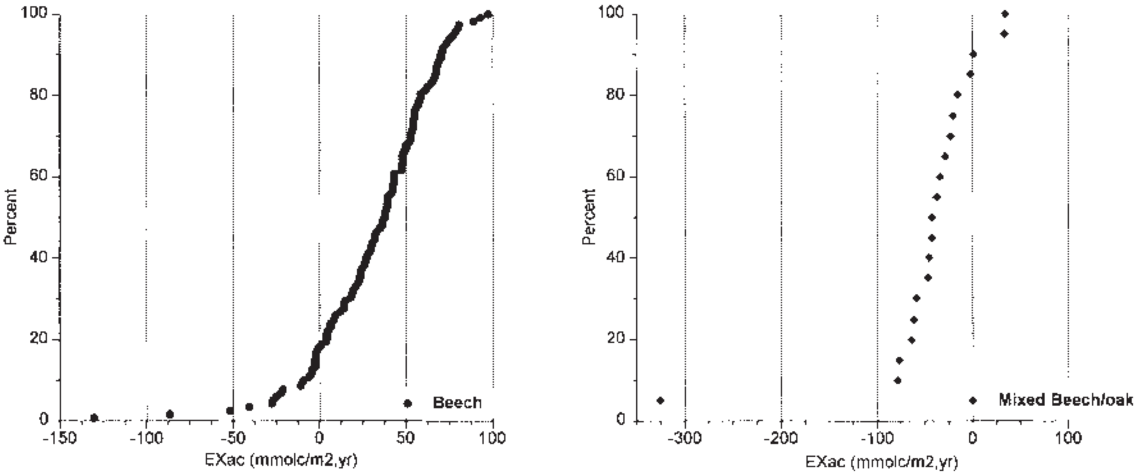
Mixed beech-oak stands: The mixed beech/oak stands has a critical load for the deposition of acid compounds of 65 -173 mmol$_c$ m^{-2} yr^{-1} and for nitrogen of 71- 120 mmol$_c$ m^{-2} yr^{-1}. The results show that for 20% of the mixed stands the critical load for acid compounds is exceed or close to zero (Fig 1b). The greater rooting depth of the mixed stands allows the trees to utilize deeper soil layers for nutrient uptake and the weathering of a greater soil volume. The mixed stands are also growing on soils with better mineral conditions and a higher base saturation. The two stands with an exceedance are growing in the part of southern Sweden, which historically have had the highest acid deposition.

Long-term sustainability

GCM/RCM driven biome modelling (Koca et al 2006) indicate that the current distribution of Norway Spruce (*Picea abies*) is likely to contract in its southern range in Sweden, Oak, Beech in particular, will extend its range further north. While spruce may be grown outside it climatically defined range it is reasonable to assume that future forestry in southern Sweden will increase it's use of deciduous trees, both as pure and mixed stands.

Projected future climate change is likely to contribute to an increased geochemical sustainability for both pure beech stands and mixed oak-beech stands. Exceedance is reduced for most stands except the poorest and most acidified. Climate change is in this context potentially beneficial but further research on the effects of an increased productivity on nutrient uptake is needed.

Figure 1: Exceedance of the critical load for Swedish beech (a) and beech/oak (b) stands (mmol$_c$/m^2,yr). Values above 0 indicate that the critical load is exceeded.



References

Braun, S. et al. 2005. Env. Poll. 137: 574-579.

Hagberg, E., Matern B. 1975. Report 15, Dept. of Forest Statistics, Swedish University of Agricultural Sciences, Stockholm, Sweden

Koca, D. et al. 2006. Climatic Change 78:381-406.

Langner, J. et al. 2000. Swedish Meteorological and Hydrological Institute, Report 58, Norrköping, Sweden.

Löf, M. 2006. Report 30. Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences.

SMHI 2007. RMK Report 111, Swedish Meteorological and Hydrological Institute, Norrköping, Sweden.

Stjernquist, I. et al. 2002. *in* Sverdrup, H., Stjernquist, I. Kluwer Academic Publishers:222-236

Sverdrup et al. 2005. J. Sust. For. 21 (2-3): 145-174.

Warfinge, P. and Sverdrup, H. 1992. Water, Air, Soil Pollut. 63:119-143.

Warfvinge, P. and Sverdrup, H. 1995. Reports in Ecology and Engineering 5:1995, Dept. of Chemical Engineering II, Lund University, Sweden.

LIKELY EFFECTS OF CLIMATE CHANGE ON GROWTH OF *FAGUS SYLVATICA*: STUDY ALONG ALTITUDINAL GRADIENTS AND COMPARISON WITH THE CO-OCCURRING SPECIES *ABIES ALBA*

Maxime Cailleret*[1] and Hendrik Davi[1]

[1] URFM, Ecologie des Forêts Méditerranéennes, INRA Avignon, 84914 Avignon, France
Tel: + 33.4.32.72.29.55 - Fax: + 33. 4.32.72.29.02 -
E-mail: maxime.cailleret@avignon.inra.fr

Introduction

Forest growth in Mediterranean mountains is limited by two major factors: summer drought at low elevation and low temperatures at high altitude (Korner 2007). As a consequence of climate change, observed trends would be the consequence of the contradictory effects of reduced frost and increased drought (IPCC 2007). On the one hand, an increase of tree growth is expected at higher elevations resulting of warming temperatures, lengthening of growing season (Badeck et al. 2004), and rising atmospheric CO_2 concentrations. On the other hand, late frost damages might not decrease (Hanninen et al. 2006). At the same time, tree growth should be reduced as a consequence of summer drought increase in sites at lower elevations (Jump et al. 2006).

The aim of this study was to analyze the effects of altitude and climate change on the growth of European beech (*Fagus sylvatica* L.) in a Mediterranean mountain. A comparative dendroclimatological study of climate-growth relationships was done. Then, the difference of growth between the North and the South faces and along elevational gradients was assessed. Effects on radial growth of recent climate change since the beginning of the twenty first century were further studied by analyzing global trends and shifts of growth optima.

Finally, a comparison with a co-occurring species was done and according to these results, a prediction of their future potential growth and distribution range in the study site was made.

Materials and Methods

The study was conducted on Mont Ventoux, a calcareous mountain in south-eastern France, where beech is located in the mountain vegetation area on the north and south face. On the North face, beech is generally associated with fir.

On the north face, 73 firs and 77 beeches were sampled along a continuous elevational transect with the same slope orientation for both species from 970 to 1530 m and were cored in autumn 2006 and 2007. On the south face, 80 beeches in 4 different plots (890m, 1115m, 1410m, and 1525m) were cored in autumn 2007. Dendrochronological analyses were made using the software CooRecorder & CDendro v5.3 (Larsson L.A. et al. 2006, Cybis Elektronik & Data AB. Sweden).

To get free from age and date effect, and to compare growth of both species, a polynomial curve was fitted against regional age mean curve of cumulative basal area. Using this function, we projected the cumulative ring area (RA) for all trees at a same age (90 years), which gave theoretical mean of annual area increase at 90 years (RA90). The same methodology was applied to study mean annual growth for the period 2000-2006.

Results and Discussion

Only results on the North face and dealing with the comparison with silver fir were presented here.

Comparison of Beech Ecology with silver fir: two co-occurring species

Climate-growth relationships: Even if these late-successional species are associated on the North face, radial growth-climate relationships were divergent.

A positive correlation was found between April temperatures and fir growth. Indeed, it causes earlier budburst and cambium activation that lengthen the growing season and increase the carbon assimilation. Inversely, a significant negative effect of maximal temperatures in April was observed for beech. An earlier budburst increases the risk of late frost damages on open buds and leaves, which can provoke a decrease of radial growth (Dittmar et al. 2006).

Drought during the first half of summer (May-July) influenced negatively ring-width of fir. In contrast, beech growth index were not related to summer rainfalls, and a positive role of May temperatures was found.

Altitude: Until the end of the 20th century, fir growth optimum was at intermediate altitude (figure 1b; S3: 1140 to 1240 m) whereas for beech it was at lower elevation (figure 1a; B1 and B2: 950 to 1230 m). Its weak presence below 950 m should probably be due to low recolonization rates from upper sites. Possible presence from about 800 to 1600 m was expected (figure 2a). This concept of optimum of growth potentialities is connected with the existence of two major limiting factors depending on altitude whose impact growth intensity : i) late frost damage and the time of growing period at high elevation and ii) summer drought in the bottom of the gradient.

Climate change effects

Global trend: In South-eastern France, temperatures increase (0.6°C to 0.7°C by decade since 1960) was not matched by rainfalls increase. Our results show that it has provoked a shift of growth optimum to higher altitudes. Since beginning of twenty-first century, most of firs showed a growth decline (52%), with mortality, whereas for beech no significant trend was shown up. In the study area, rising temperatures and decreasing rainfalls (4-27%) are predicted (IPCC 2007). These growth trends would logically go on.

Effects on climate events: An earlier budburst results in an increase of damage probabilities due to late frosts (Hanninen et al. 2006). As a consequence, growth of beech at high altitude might be not as much favored as it could be by the temperature increase.

2003 summer was exceptional for the intensity and the length of the heat-wave but it occurred at the end of growing season (most in August). No significant growth decrease was observed during this year because most of the growth rings were produced earlier (Bouriaud 2004). A significant growth decrease took place in 2004 due to the reduction of carbohydrate storage and to the reduced rainfalls during June and July 2004. We found a higher negative response for beech than for fir.

The higher sensitivity of beech growth to climate events may be due to the non persistence of its leaves.

Likely modification of species' range

The elevational gradient can be schematized as a curve where the two majors limiting factors progress exponentially with the altitude (figure 2a, 2b). The number of frost days and their intensity increase exponentially with the upward shift in altitude. Toward lower altitudes, the frequency, intensity and duration of summer drought increase exponentially owing to the mix of rising of temperatures and decline of rainfalls.

In lowest altitudes fir would disappear (figure 2b), but the expected increase of heat-waves (Meehl and Tebaldi 2004) will affect also beech vitality. At high elevation, the upward shift of beech may probably be limited by late frost damages. Silver fir will completely take advantage of the temperature rising and the lengthening of growing season. Distribution range would be reduced since their upward progression thanks to dispersion which will be probably lower than the rising of temperatures.

If extreme events were not taken in account, *Abies alba* is predicted to face higher risk of extinction than *Fagus sylvatica* (Ohlemüller et al. 2006). But the probably increase of late frosts, heat-waves frequency and intensity would put beech in a disadvantageous situation.

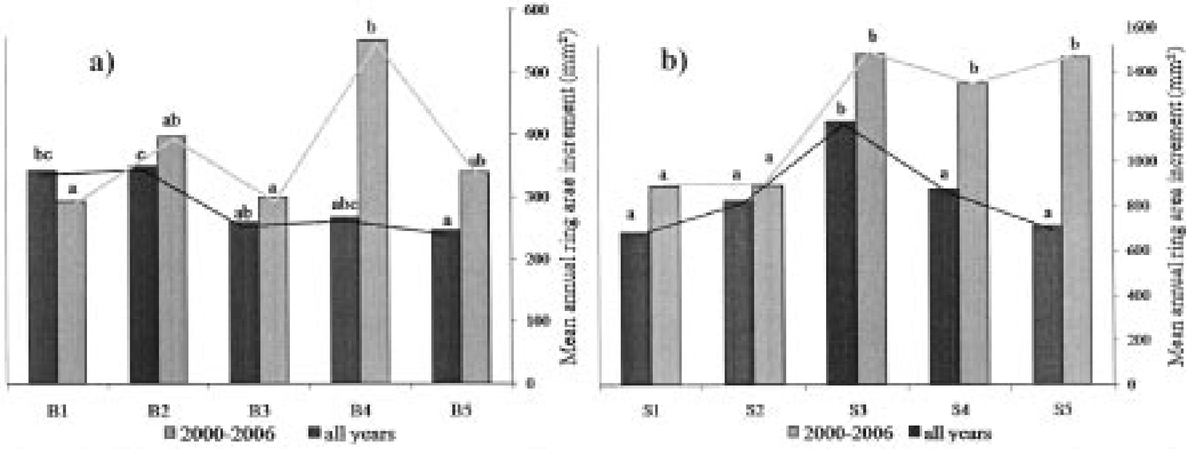


Figure 1: Altitude effect on mean annual ring-area increment (mm²) of *Fagus sylvatica* (a) and *Abies alba* (b) for all the period studied (black histogram) and for the period 2000-2006 (grey histogram). Elevational levels are the altitudinal classes (B1 and S1: low altitude to B5 and S5: high altitude). Different letters indicate significant differences between means for the same period (P<0.1, t.test).

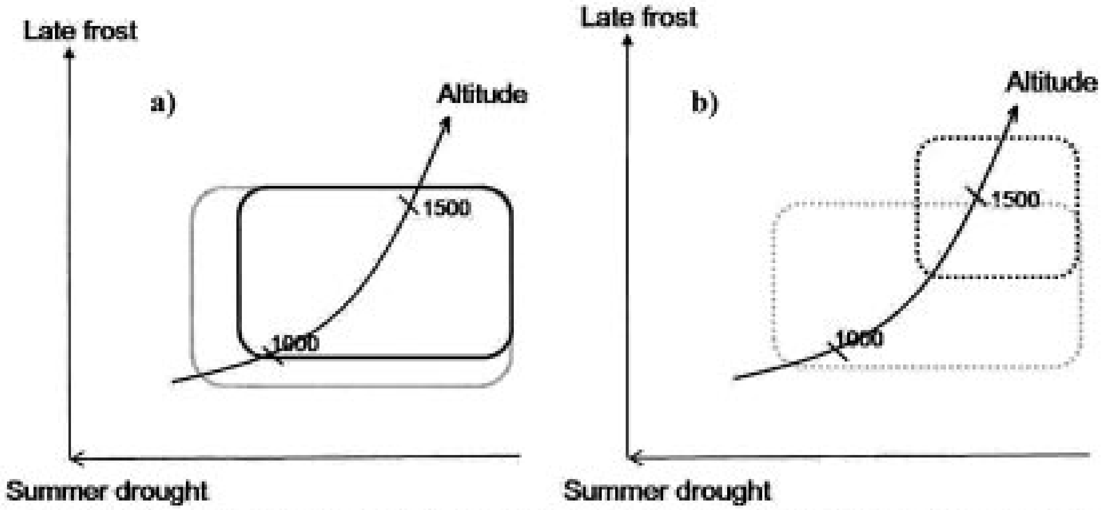


Figure 2: Actual (a) and likely future (b) distribution range of silver fir (black) and common beech (grey). The two major limiting factors are late frost (number and/or intensity), and summer drought (frequency, intensity and/or duration). The curve is the elevational gradient of the North face of the Mont Ventoux.

References

Badeck, F.W., et al. 2004. New Phytol. 162: 295-309.
Bouriaud, O., et al. 2003. Trees 18: 264-276.
Dittmar, C., et al. 2006. Eur. J. For. Res. 125: 249-259.
Hanninen, H. 2006. Tree Physiology 26: 889-898.
Jump, A.S., et al. 2006. Global Change Biology 12: 2163-2174.
Körner, C. 2007. Trends Ecol. Evol. 22: 569-574.
Meehl, G.A., Tebaldi, C. 2004. Science, 305: 994-997.
Ohlemüller, R., et al. 2006. Global Change Biology 12: 1788-1799.

BUDBURST OF EUROPEAN BEECH IN VENTOUX FOREST: A MODELLING APPROACH OF TRADE-OFF BETWEEN CARBON INPUT AND FROST RISKS

Hendrik Davi*[1], Marion Gillmann[1], Thomas Ibanez[1], Maxim Cailleret[1] and Annabelle Amm[1]
[1]INRA-UR629. Unité de Recherches Forestières Méditerranéennes (URFM), Domaine Saint Paul Site Agroparc, F-84194 Avignon Cedex 9.
tel: +33-04.32.72.29.99 fax: +33-04.32.72.29.02 email: hendrik.davi@avignon.inra.fr

Introduction

Phenology consists in the study of cyclical biological events, such as flowering, budburst, breeding, and dispersion. These phenological observations can be interpreted with respect to climatic conditions. For vegetation, it is an important adaptive trait since it determines duration and timing of the growing season as well as the period of reproduction (Chuine et al., 2000) and is also shown to be a major determinant of plant species ranges. Change of phenology is one of the most easily observed responses to climatic change (Parmesan & Yohe, 2003). As budbreak determines the length of growing season for deciduous species, it is also an important factor determining their carbon budget. Davi et al. (2006) showed that for deciduous species, the length of the leafy period might increase by 38 days from 1960 to 2100 (early budburst contributing for 55% and delayed leaf fall for 45% of this increase).

Fagus sylvatica budburst is late in plain and is quite early in high altitudes while its growth is negatively affected from earlier budburst due to late frost. This behaviour is probably due to the necessity to increase as more as possible the vegetation length.

In this presentation, we first compared beech budburst with other species, within plains using a French database and along an altitudinal gradient. Then, the variations of budburst with altitude were discussed from an adaptative perspective using simulations obtained from a process based model.

Material and Methods

The French database RENECOFOR

The RENECOFOR-network was created by the French National Forest Board (Office National des Forêts, ONF) in 1992 in order to complete the existing French forest health monitoring activities. In each plot, phenological observations were performed once a week on 36 trees representative of the plot in terms of species, age and structure. Budburst date was defined as the date when 50% of the trees have the buds open over at least 20% of the crown of each tree. To compare *Fagus* with other species, 1186 budburst dates were analysed for six deciduous species from 1997 to 2005.

The altitudinal gradient

The altitudinal gradient was studied on Mont Ventoux (44°11'N; 5°17'E), a mountain located at the south-western of the Alps (1909m). In 1850, it was almost entirely deforested due to pastoral and forest over-exploitation. The decrease of grazing combined with the reforestation efforts undertaken in the 20th century using pines made it possible for post-pioneers (*Sorbus aria*, *Acer opalus*) and shade-tolerant species (*Abies alba* Mill. and *Fagus sylvatica* L.) to gradually recolonize the planted stands. Climate is typical of low altitude mountains with Mediterranean influences with 9.25°C mean annual temperature and 1068 mm mean annual rainfall at 1000 m. Two gradients were further studied: 4 stands on the north face and 4 stands on south face (respectively at 890m, 1115m, 1410m, 1530m gathering 90 beeches).

Measures

A notation of bud development was carried out for each tree every week (14 times in 2006 and 18 times in 2007) by distinguishing the bottom and the top of the canopy. Six marks were used to quantify accurately budburst dynamics. The position, altitude, diameter and height of each tree were recorded. Temperature and relative humidity were recorded using eight mini meteorological stations Prosensor V2 (U23-001 ±0.2°C; ±2.5% RH). All the stations were put at 1.5 m from the ground in a cleared stand inside a case protecting the sensors against direct radiation and overheating.

CASTANEA Model

CASTANEA is a physiological process-based model simulating the carbon and the water balance in forest stands. The main simulated output variables are the canopy photosynthesis, maintenance and growth respiration, organs growth, soil heterotrophic respiration, transpiration, and evapotranspiration. Phenological stages (budburst, end of leaf growth, and start of leaf yellowing) and leaf growth depend on degree days (i.e. heat amount accumulated). Budburst is simulated following the equation 1-3:

$$\text{(1)} \qquad \mathrm{R}_{\mathrm{frcBB}} = \begin{Bmatrix} \mathrm{T} & \text{if } \mathrm{T} > \mathrm{T}_1 & \textit{and} & N > Nstart \\ 0 & \text{if } \mathrm{T} \leq \mathrm{T}_1 & \textit{or} & N < Nstart \end{Bmatrix}$$

where R_{frcBB} is the rate of forcing for bud break, T the mean daily temperature, T the base temperature, N the day of year and N_{START} the date of onset of rest.

$$\text{(2)} \qquad S_{\mathrm{frcBB}} = \sum_{N_{\mathrm{START}}}^{N} R_{\mathrm{frcBB}} \qquad \text{if} \qquad \mathrm{S}_{\mathrm{frcBB}} < \mathrm{F}_{\mathrm{critBB}}$$

$$\text{(3)} \qquad N_{\mathrm{BB}} = \mathrm{N} \qquad \text{if} \qquad \mathrm{S}_{\mathrm{frcBB}} = \mathrm{F}_{\mathrm{critBB}}$$

with S_{frcBB} the state of forcing, F_{critBB} the critical value of state of forcing for the transition from quiescence to the active period and N_{BB} the day when bud break occurred. Effects of frost are taken into account when Tmin is below -3°C (Dittmar et al. 2006). Complete description and validation of the model were given in Dufrêne et al. (2005).

Results and Discussion

Renecofor data base

In plain, *Fagus* budburst occurs later (Julian day 114) than other deciduous species (110, 107, 112, 107, 110 respectively for *Betula*, *Carpinus*, *Castanea*, *Corylus* and *Quercus*). Correlation coefficient (Coef) between average temperature from January to March and average budburst date is higher for *Fagus* ($r=-0.5$) than for *Quercus* ($r=-0.32$). Furthermore, *Fagus* is the only species for which Coef is higher with April temperature ($r=-0.58$) than with average temperature since January. This last result shows the importance of frost on beech phenology.

Altitudinal gradient

Budburst occurs later in high altitudes (Fig. 1a) and later in 2006 than in 2007. Estimated state of forcing (with $N_{START}=74$ and $T_1=0$) is the same between 2006 and 2007, but change between North and South faces and with altitudes (Figure 1b). These observations could be the result of adaptation to altitude and exposition. Indeed these changes allow to maximize the carbon gain by increasing vegetation length (early budburst), but avoiding frost damages that occur Tmin is below -3°C (Fig 2).

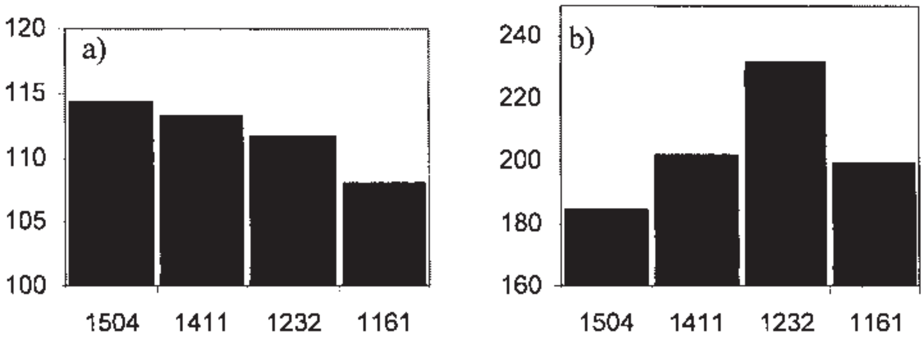


Figure 1: a) Mean date of budburst and b) estimated state of forcing (°C) in function of altitude

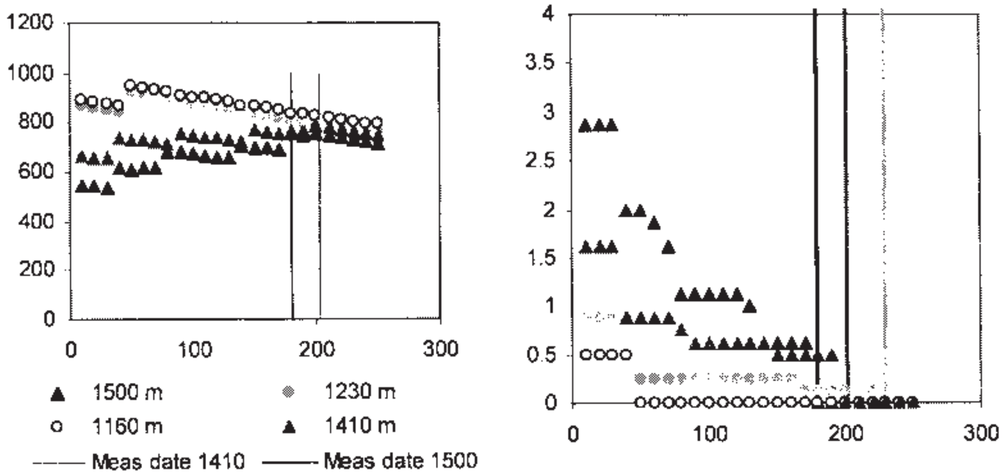


Figure 2: Sensitivity of a) GPP-R ($g_C\ m^{-2}\ y^{-1}$) b) number of days with Tmin<-3°C to simulated state of forcing (°C) in average from 2000 to 2007. Vertical bars indicate the measured state of forcing on four altitudes.

To conclude, state of forcing of Beech budburst appears to be adapted to the elevation with a date of budburst selected to avoid frost damages. This result is consistent with the fact that budburst date is mainly determinate by April temperature (high correlation in the French database and delayed NSTART of Julian Day 74).

References

Chuine I et al. 2000. J. Ecol., 88, 1 :12.
Davi, H. et al. 2006. Agricultural and Forest Meteorology, 141, 35-56.
Dittmar, C., et al. 2006. Eur. J. For. Res. 125: 249-259.
Dufrêne et al. 2005. Ecological modelling. 185(2-4), 407-436.
Parmesan C, et al. 2003. Nature 421: 37–42.

PRIMARY PRODUCTIVITY CHANGES FOR A THIRTY-EIGHT-YEAR PERIOD IN A NATURAL BEECH (*FAGUS CRENATA*) FOREST IN THE NAEBA MOUNTAINS

Yoshitaka Kakubari*[1], Masaaki Naramoto[1], John Tenhunen[2], Reiner Zimmermann[2]
and Yukihiro Chiba[3]

[1] Institute of Silviculture, Department of Forestry and Environment, University of Shizuoka,
Ohya, Suruga-Ku, Shizuoka, 422-8529, Japan
Tel:+81-54-238-4840, Fax:+81-54-238-4841, e-mail:afykaku@agr.shizuoka.ac.jp
[2] Plant Ecology, Univ. Bayreuth, Germany
[3] FFPRI, Tsukuba, Japan

Introduction

Primary production studies of natural Japanese beech (*Fagus crenata*) forests were started in the 1960's, and the study in the Naeba Mountains by Niigata University group was chosen as one of the supporting programs of the Japanese *IBP/PTF*(International Biological Program/ Productivity of Terrestrial Forest community) Subcommittee (Yamada and Maruyama 1962; Maruyama, 1971,1977; Kakubari, 1977,1987,1988,1991). Since the *IBP* in the Naeba Mountains, eight permanent plots were monitored to evaluate an altitudinal gradient effects from 550 m to 1500 m on structure and production of *Fagus crenata* forest stands of the Japan-sea side (Kakubari 1987). Beech plantations are not common in this country, also were dealt with by Tadaki *et al.* (1969). The research of primary productivity change for a long time monitoring in Naeba related to response along climate gradients are relevant to national beech forest and global studies of carbon balances by use of eco-physiology and remote sensing (Kakubari *et al.*2000,Tenhunen *et al.* 2000, Kubota *et al.*2005, Wang *et al.* 2008,Nishigami *et al.* 2008). This paper introduces the distribution of primary productivity along an altitudinal gradient by the use of data of thirty-eight years, from 1970 to 2007.

Study Site and Methods

The Naeba Mountains are located at about 36 51'N and about 138 41'E in the southern part of Niigata Prefecture. On the northern slopes of the Naeba Mountains, beech forests are distributed over a range of altitude between 550m and 1,550m, corresponding to a range of warmth index 45 – 85 (Kira, 1949). Bed-rock in the study area is predominantly andesite and basalt, on which the brown forest soil of a moderately moist type has formed. Eight permanent plots ranging from 800 m^2 to 2200 m^2 were established in 1970 as shown in Table 1. Plots 1, 7 and 8 were close to the lower and upper limits, respectively, of beech forests in this area.

Table 1. Physiographical features of eight permanent plots along the altitudinal gradient in the Naeba Mountains since 1970.

Plot no. and Name	Altitude(m)	Age(year)	Plot size(m^2)	Start of survey	GPS
1 Kiyotugawa	550	250	2000	14.May.1970	N36.55.21,E138.45.57
2 Nagasaka	700	250	2200	15.May.1970	N36.54.58,E138.46.20
3 Sotonokawa	700	250	2000	24.May.1970	N36.55.06,E138.46.18
4 Yakio	900	250	2000	11.July.1970	N36.52.20,E138.45.51
5 Yakio	1100	250	800	10.July.1970	N36.52.21,E138.45.19
6 Yakio	1300	300	2000	14.June.1970	N36.52.03,E138.44.49
7 Kaguramine	1500	300	1000	13.June.1970	N36.50.31,E138.44.02
8 Yakio	1500	300	1400	9.July.1970	N36.51.41,E138.44.02

At 700 m in altitude, the deep winter snow accumulation (3-4m in depth) was observed to remain until mid-May; beech leaves began to flush in late April or early May, and the start of autumn-coloring of leaves took place in late October. Corresponding seasons at 1500 m were early June (snow melting), late May – early June (leaf flush), and early October (leaf coloring). The duration of the growing period was estimated to be 183 days at 550 m, 173 days at 700 m, 161 days at 900 m, 153 days at 1100 m, 139 days at 1300 m, and 127 days at 1500 m. All living trees on the plots (DBH>4.5 cm) were numbered, and the positions of stem bases and crown projections were mapped. Each tree was marked with a band of red around the stem at breast height (130 cm), and their DBHs, aboveground height, and species were recorded. Trees which died during one year and those which newly-reached the size of 4.5 cm DBH in the same year were recorded each autumn. The upper layer of the canopies of the eight plots consisted mainly of beech with occasional mixtures of a small number of such species as *Quercus mongolica var. grosseserrata, Magnolia obovata, Kalopanax septemlobus, Betula grossa*, and *B.ermanii*. The second layer, about 5 m tall, contained *Acer palmatum, A. refinerve, A. sieboldianum, Acanthopanax sciadophylloides, Fraxinus mandshurica, Magnolia salicifolia*, and so forth. The mean tree height decreased with increasing altitudes at a rate of 30—60% per 800 m.

Tree mortality and stem diameter increment, 1970—2007 and estimation of biomass and biomass increments

The number of living trees on all plots totaled 732 at the first census in 1970 (Kakubari, 1988). During the thirty-eight years, until the fall of 2007, 450 trees were found as standing dead or windfall trees caused by heavy storm in 1982, whereas stems newly-entered the tree class having a DBH of over 4.5 cm. The total number of thus became 1089 in November 2007. The difference of 33 stems newly-entered the tree class and died again.

Based on the allometric correlation between various tree dimensions and D_2H (Satoo, 1962), the stand biomass was estimated. The allometric equation (Kakubari, 1988, Kakubari 1991) was;

$$\mathrm{Log}\ Y = h \log (D_2H) + K \qquad (1)$$

Table 2. Coefficient (*h* and *k*) of Eq.(1) used for the calculation of above ground biomass at different altitudes.

Altitude(m)		Dependent variables					Sources
		Stem Wts(kg)	Stem Volume(m^3)	Branch Wts(kg)	Leaf Wts(kg)	Leaf Area (m^2)	
1500	*h*	0.9047	0.9123	0.9193	0.7414	0.6320	*1
	k	-1.3316	-4.082	-2.058	-2.3914	-0.7396	
1300	*h*	0.9145	0.9042	1.0192	0.6721	0.6291	*2
	k	-1.2772	-4.0498	-2.2982	-2.0186	-0.6843	
1100	*h*	0.9307	0.9402	1.3648	0.6229	0.7086	*3
	k	-1.3946	-4.1887	-3.8424	-1.9747	-1.1519	
900	*h*	0.8895	0.9003	1.0443	0.7239	0.6113	*4
	k	-1.2144	-4.0055	-2.3472	-2.2078	-0.5407	
700	*h*	0.9334	0.9432	1.0218	0.7916	0.6685	*5
	k	-1.4011	-4.1843	-2.5141	-2.7089	-0.8523	

*1,Kakubari et al.(1970), *2,Maruyama and Yamada (unpublished), *3, Kakubari(unpublished), *4, Yamada and Maruyama (1962), *5, Maruyama et al. (1970)

The dry weight of stems, branches and leaves and stem-wood volume and leaf area per tree were taken as the dependent variable (Y). The values of two coefficients in the equation used in the calculation, h and K, are shown in Table 2. The calculation of biomass was made for two different times, spring of 1970 and fall of 2007, on the assumptions, 1) that the allometric correlation of Table 2 did not change with time, 2) that trees of species other than beech also satisfied the same allometric relationship, 3) that tree-height curves did not change during the period concerned, and 4) that root biomass was equal to 20% of the above ground wood biomass. Because Plot1 (550m) lacked destructive sampling data obtained at the same levels of altitudes, the calculations for this plot were made tentatively using the coefficients for 700m.

The estimated biomasses in the spring of 1970 ranged from 342.0 t./ha, being more or less similar between 700m and 1100m (339.6 t/ha) but much smaller at higher altitudes. Except for somewhat doubtful, smaller value at 550m, that biomass decreased with increasing altitude was apparent. The difference in biomass of trees that survived throughout the thirty-eight years gives the biomass increment. Its rate was greater than –2.6 ~1.00 t./ha.yr between 550m and 900m, but was less –1.6 ~ 0.36 t/ha.yr above 1300m. The negative values of "Biomass increments" indicate the loss of stand biomass due to death and to windfall trees. Subtracting this loss and adding the biomass of newly counted trees to the increment of the living biomass, the net increase in stand biomass was calculated. The rate of net biomass increase was the largest on plot 4 at 900m, and generally was greater at lower altitude plots than at higher altitude plots.

Altitudinal changes in production rates

The rates of net production were approximated by the sum of the rates of net biomass increase and litter-fall, neglecting the consumption by grazing of herbivores. The gross production rates were obtained by adding the rates of community respiration to that of net production. The results were summarized and are averaged rates of gross and net productions during the period of 1970 to 2007. All of the net production, community respiration and gross production tended to culminate at the middle altitudes around 900m. Because each level of altitude was represented by one or two plots, the altitudinal trend may not be greatly reliable, but it is not unreasonable that a plant community should exhibit its maximum capacity near center of its distribution range along a certain environmental gradient. The estimated net production was approximately 3.1 at 1500m, 5.2 t at 700m, decreasing by about 40% with increase of 800m. The reasons of decreasing of primary productions along the different elevations comparing with the growing seasons, leaf area and photosynthetic capacity etc. at the taken data in the Naeba Mountains.

References

Maruyama, K. 1971 Mem.Agric.Niigata Univ. 9:85-171.
Maruyama,K. 1977 J.Int.Biol.Program Synth.16:186-212.
Nishigami,A et al 2008 Jpn.For.Plan.13:225-232
Kakubari et al. 1970 Niigata Norin Kenkyu 22:43-55.
Kakubari,Y. 1977 J.Int.Biol.Program Synth.16:201-212.
Kakubari,Y. 1987 Bull,,.Tokyo Univ.For. 76:107-162.
Kakubari,Y. 1988 3rd. IUFRO Beech Symposium in Zvolen 183-191
Kakubari,Y. 1991 J.Jpn.For.Soc. 73:370-374.
Kubota,M. et al. 2005 Tree Physiology 25:537-548
Satoo,T.1962 J.Jpn.For.Soc. 44:267-272.
Tadaki,Y. et al. 1969 J.Jpn.For.Soc. 51:331-339.
Tenhunen j. et al 2000 IAVS43 Nagano
Yamada,M. and Maruyama,K.1962 Trans.72nd meet.Jpn.For.Soc.:245-248.
Wang,Q. et al. 2008 Tree Physiology 28:277-285

IS *FAGUS CRENATA* EXPANDING NORTH-EASTWARDS IN HOKKAIDO? -IMPLICATIONS FROM FOREST AGE STRUCTURE AND DISTURBANCE HISTORY-

Tetsuya Matsui*[1], Kanji Namikawa[2], Ryota Goto[2], Makoto Kobayashi[3] and Shigeo Kuramoto[1]

[1]Forest Ecology and Diversity Group, Hokkaido Research Station, Forestry and Forest Products Research Institute, 062-8516, Sapporo, Japan
Tel: + 81.11.590.5522 - Fax: + 81.11.851.4167 - E-mail: tematsui@affrc.go.jp
[2]Biological Laboratory, Sapporo College, Hokkaido University of Education, Sapporo, Japan
[3]Graduate School of Environmental Earth Science, Hokkaido University, Sapporo, Japan

Introduction

Fagus crenata Blume (Buna or Siebold's beech) is one of the most dominant tree species in the cool-temperate forests in Japan. The southern limit of its range lies in Mt. Takakuma in the southern island of Kyushu (31°29' N, 130°49' E), and northern limit does in the Kuromatsunai / Rankoshi region (42°39' N, 140°25' E), southern part of the Hokkaido island.

Forests of *F. crenata* retreated to middle part of Honshu (main island of Japan) in the last glacial period had started northward expansion after the last glacial period and reached the northern end of Honshu *ca.* 9,000 years ago (Tsukada 1982). The species arrived in southernmost Hokkaido of Hakodate at *ca.* 6,000 years ago (Igarashi 1994; Kito 2003) and then reached Mt. Kariba, 30 km west of the Kuromatsunai lowland, at *ca.* 1,000 years ago (Igarashi 1994). These facts suggest that the migration rate of *F. crenata* was *ca.* 230 m/year in Honshu (Tsukada 1982), *ca.* 40 m/year from Hakodate to Mt. Kariba and *ca.* 12 m/year from Mt. Kariba to the Kuromatsunai lowland. This reduction in northward expansion speed indicates that one or more factors have hindered invasion of this species to the existent forest stands primarily dominated by *Quercus mongolica* var. *grosseserrata*.

Although *F. crenata* primarily forms continuous forest stands in south-west of the Kuromatsunai lowland (*i.e.*, in their range), it has been known that they can also be found sporadically in north-east of the lowland and in the Horobetsu Mountains in the Rankoshi town (Kito 2003; Tatewaki 1948). Furthermore, we recently found some outlying populations other than those reported previously in the Horobetsu Mountains. These facts arise a hypothesis that *F. crenata* is still expanding its range towards north-east of Hokkaido.

Among those outlying *F. crenata* stands in the Horobetsu Mountains, the Tsubamenosawa Buna forest (elevation *ca.* 550-620 m, N42°47'44", E140°23'47"), on the eastern side of Horobetsu Mountains, has been well known as the northernmost outlying population (Kobayashi & Watanabe 2003; Watanabe 1987). However, no clear growth inhibition has been reported in the forest. Kobayashi & Watanabe (2003) estimated age of *F. crenata* to be between 190 and 250 years old, by diameter growth comparison between 1986 and 2002. This suggests vigorous regeneration of *F. crenata* in the forest. However, there were still some questions such as on the establishment process or regeneration characteristics of the outlying forest stands.

Objectives of this study were therefore: (1) to clarify age structures of an outlying northernmost forest stand, (2) to elucidate regeneration characteristics of *F. crenata*, and (3) to discuss whether or not the trees are still expanding their range towards north-east of Hokkaido .

Materials and Methods

The Sannosuke Buna forest (elevation ca. 350-50 m, N 42°46' 48", E 140°23' 43") was one of the outlying forest stands, which lies *ca.* 4 km south of the Tsubameno-sawa Buna forest. The area of the forest was *ca.* 3 ha, which was larger than the Tsubameno-sawa Buna forest (ca. 2 ha).

Field sampling was executed in a 150 m (longitudinal) x 50 m (transversal) study area, within which topographical surface was surveyed at a spatial scale of 2.5 x 2.5 m grid. Diameter at the breast height (DBH) was measured for each tree over 10 cm in DBH. X-Y coordinates of the trees in the study area were recorded.

Wood pieces were sampled from fallen logs, with diameter at the breast height (before fallen down) larger than 10 cm, to estimate major woody species composition in the past.

Increment cores were extracted from each tree over 10 cm DBH in the study area. Samples were taken from the lowest possible part of each tree. Five *F. crenata* juveniles (*ca.* 2 m in tree height) were sampled and disks were made for every 20 cm from the ground level, to estimate the years taken to reach the cored height.

The number of tree rings in each increment core was counted and each ring width was measured using the aid of DENDROTAB 2003 (Walesch Electronic) and T-Tools Pro (IML GmbH), with the minimum measurement to 0.01 mm. When a core did not reach the chronological centre, the number of rings from the chronological centre to the innermost ring of the core had to be estimated, following the methods proposed by Norton (1987) and Duncan (1989).

Results

The study area was on relatively steep slope with inclination of 20 - 40 degrees. Micro topography in the study area (2.5 m^2 grid scale) was undulating between steep slope and gentle slope, although a general trend of the slope was consistent as a south-west slope, on the eastern side of the Horobetsu Mountains (892 m).

A total of 394 trees were used for tree age estimation, of which 239 trees (*ca.* 60 %) were *F. crenata*. Age class distribution revealed that all the trees between 60 and 70 years old had the highest proportion, and so as for *F. crenata* trees. The age class distribution and the spatial patterns of *F. crenata* trees showed that: (1) trees younger than 80 years old were ubiquitous in the study area, (2) trees between 80 and 120 years old mainly grew on the lower part of the study area, around which convex slope suddenly became steeper, (3) trees older than 120 years mainly grew on the upper part of the study area (Fig. 1). Species identification of fallen logs showed that the number of *F. crenata* trees was much smaller than expected in the past and *Quercus mongolica* var. *grosseserrata* had higher proportion.

Discussion

Existence of small-scale, undulating, convex and concave shaped slope, which extends horizontally beyond the study area over *c.* 100 m, suggested that there was soil disturbance event(s) in the past, and the study area should have been affected in its topography.

Judging from the present tree age structure, landform, past species composition and recorded past disturbance, it was presumed that (1) *F. crenata* between 80 and 120 years old regenerated after the alleged land slide event, and (2) the trees younger than 80 years old, especially a majority of the trees of 60-70 years old in the study area, started growing vigorously after the canopy disturbance, probably caused by the historically large typhoon Touyamaru, which hit Hokkaido in 1954.

We concluded that the past disturbance events facilitated the establishment and growth of *F. crenata* in Sannosuke Buna forest, and there was no evidence denying the hypothesis that *F. crenata* has been vigorously growing and expanding its range limit towards north-east in Hokkaido.

Acknowledgment

We sincerely thank Dr Norio Kito for the permission to use his original *F. crenata* map in the Kuromatsunai region.

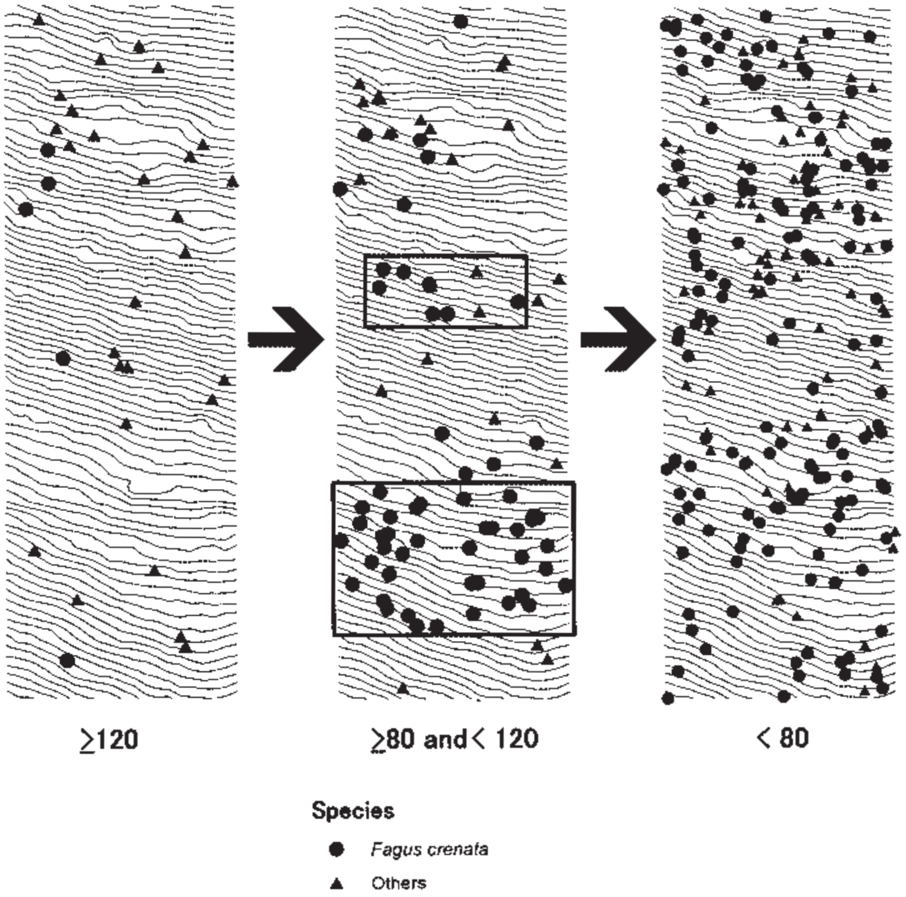


Figure 1: Spatial distribution of tree individuals (cored and age was estimated) in the study area: (a) trees older than or equal to 120 years old, (b) trees between 80 and 120 years old, and (c) trees less than 80 years old. Map (a) indicates that first *F. crenata* trees colonised on the upper part of the study area. Map (b) indicated that *F. crenata* trees vigorously grow on the convex-shaped slopes (framed by the two squares), after the landslide. Map (c) indicates that *F. crenata* trees vigorously regenerated, presumably after the canopy disturbance caused by the typhoon Toyamaru in 1954.

References

Duncan, R.P. 1989. New Zealand Natural Sciences 16:31-37.

Igarashi, Y. 1994. Forest Tree Breeding of Hokkaido 37:1-7.

Kito, N. 2003. Shinrin Kagaku 37:46-50.

Kobayashi, M., and Watanabe, S. 2003. Global Environmental Research 5:1-23 (in Japanese with English abstract).

Norton, D.A., et al. 1987. New Zealand Journal of Botany 25:373-383.

Tatewaki, M. 1948. Seitaigaku-kenkyu 11:46-51.

Tsukada, M. 1982. Japanese Journal of Ecology 32:113-118.

Watanabe, S. 1987. Beech Forest in the Northern Range Limit (Hokugen no Bunarin, in Japanese). Hokkaido Ringyo Kairyo Fukyu Kyoukai, Sapporo, Japan.

BEECH, A KEY SPECIES FOR THINKING ABOUT CLIMATE CHANGE ADAPTATION

Myriam Legay*[1], Brigitte Pilard-Landeau[2] and Alain Valadon[3]

[1] Interface INRA/ONF, Centre INRA de Nancy, 54 280 Champenoux, France
Tel: + 33.3.83.39.40.51 - Fax: + 33.3.83.40.22- E-mail: legay@nancy.inra.fr
[2]ONF, Direction territoriale Ile de France - Nord-Ouest, tel 00 33 3 44 40 11 94, E-mail : brigitte.pilard-landeau@onf.fr
[3] ONF, Conservatoire Génétique des Arbres Forestiers, USC ONF-INRA, Centre de recherche d'Orléans, tel +33.2.38.41.78.32 - Fax 00-33-(0)2 38 41 48 00 –
E-mail: alain.valadon@onf.fr

Introduction

Common beech is the third species in French forest after *Quercus sessiflora* and *Q. robur* for covered area (IFN, 2005), with 11 % of the present standing volume. Beech is present from mild oceanic Brittany to the Vosges Mountains, and from northern lowlands high forests to Mediterranean heights, on calcareous superficial soils or acid sandy soils as well. At low elevations in South-West and in South, beech is excluded by climatic conditions. France provides a good sample of ecological conditions suitable versus unsuitable for this species. Climate warming taken apart, some environmental drivers: maturation dynamics, herbivory pressure, or decreasing silvicultural investments, tend to favour beech in many French forests. But the future of beech under climate change is a matter of concern for forest managers.

Our approach

Several studies of beech temporal or spatial response to climate were carried out at the scale of France. On the basis of this scientific material, we assume that beech is an inspiring model to study climate change impacts on French forests. The dialogue between scientific results and management issues on this case rise interesting questions. Among them, interrogations about adaptation abilities take a great place. How to cope with an urgent need for action in a context of great uncertainty? In a third part we expose the first adaptation axis proposed for the French public forests.

Beech observed response to climate and expected response to global changes in the French context

Radial growth and observed niche: a clear response to climate

Using the French National Forest Inventory database, Badeau built a niche model (2004). Climatic water deficiency during the growing season was the best predicting factor of beech presence or absence. The same factor appears in dendroecological studies. The variation of beech ring widths is known to show a clear response to year-to-year climate variability (Dittmar 2003). A dendrochronological survey carried out in the 15 beech plot of RENECOFOR network[1], shows that soil water deficiency in June or July is the main growth limiting factor. The drier the site is, the more radial growth appears to be sensitive to this factor (Lebourgeois 2005). The climatic signal is clearer in beech than in oak (ref). According to this climatic behaviour, a large retreat of the species is expected, as shown by the projected niche in 2100 under B2 scenario (Badeau 2004).

Seynave (2008) showed that spatial patterns of potential height growth spatial variability are also explained mainly by climatic parameters. The relevant climatic factors are spring cold

---

[1] French Permanent Plot for the Monitoring of Forest Ecosystems

(negative effect), summer heat (negative effect) and winter climate. This model suggests complex effects of climate warming. A general growth decline is not systematically observed at the vicinity of the range boundary. Similar results are shown when considering radial growth (Legay 2008).

From growing productivity to decreasing competitiveness ?

Several studies have shown evidence of an increasing productivity, in France like in many European forests. Bontemps showed a 50% increase of dominant height growth in the northeastern France over the last century (2006). This trend could appear contradictory with the expected decay of the species. On one hand the contribution of climate warming among other potential drivers (increasing CO_2 concentration, fertilising pollution) has not been evaluated yet. On the other hand increasing water deficiency could balance growth stimulating factors, the sooner where the vegetation period is the drier. A slow down of the productivity increase observed by Bontemps during the last decade in the west could suggest such a phenomenon. Projections from physiological models simulate such a change of trend in north-western lowlands, with a productivity plateau reached by the middle of the century (Loustau 2004).

A case study of dilemmas facing forests managers in the context of global change

The beech paradox

In order to survey the process of the expected retreat of beech, an interesting approach consists in studying its behaviour at its range margin. An altered fitness is expected there, especially after extreme drought events. A severe drought occurred in 2003, followed by decline or mortality, but few reports concern beech stands. Generally speaking, decline or mortality events following drought events are less common for beech than for oak. This paradox underlines a key issue for forest managers, who are supposed to make rational decision today for the next century: shall we change beech for another species, on the basis of simulations, or shall we wait for massive mortality events?

The adaptability margin

The main question concerns the adaptability of the species to the expected high speed climate change. The intrapopulation diversity of beech is high, and evidence for one generation adaptation to warmer conditions was given by Jump (2006) at the south beech boundary in Spain. But this adaptability has to be investigated more in details: what is its potential magnitude? Is it equally distributed among populations? Plasticity might also be investigated through existing European provenance tests network that provides samples of provenances submitted to a different climate then their original one. An interesting practical issue concerns the genetic quality of forest reproductive material, the choice of natural regeneration methods promoting high within-stand diversity, and the development of silvicultural methods enhancing the selection of stems with a high ecological plasticity or resistance to drought (which would not necessarily be selected on classical growth criteria), all choices valorizing local adaptation capacities.

Moving the provenance northward ?

Another dimension of intraspecific variability is existing inter-population differentiation. Shall we promote species adaptation to changing conditions with provenance transfers in order to valorize regional adaptation capacities? Due to high gene flows between forest tree stands, uncontrolled and irreversible consequences might be expected. Besides, the risk of giving way to chaotic provenances transports has to be taken into account. Such a decision must be submitted to a strong scientific evaluation and preparation. The first urgent step of this evaluation is to engage an international partnership to collect and analyse existing international provenance tests.

First adaptation axis for French public forests

Forest managers face this dilemma: act without delay to mitigate climate change impacts, but with great uncertainty concerning the change scenario. Let us expose the main axis of adaptation recommended for French beech stands, taking as a reference the north-western lowlands, an area of high quality beech production.

- Restrain the dominance of beech to optimal sites: the research of a practical bioclimatic criterion of site suitability for beech is in progress. In north-western France, for the moment beech is kept as the main objective species where the maximum content of the soil is estimated higher than 100mm. In other cases, sessile oak will be preferred for the next stand renewing.
- Improve natural regeneration techniques and FRM management in order to favour and valorize intraspecific diversity.
- Accelerate the renewing of the oldest stands (more than 150 years old), supposed to be less resistant to extreme climatic events. The change of generation promotes acclimatising and adaptation to warmer conditions. In northwest lowlands, the renewing rate will double during the next decades.
- Adapt silvicultural guidelines, to obtain stands with a reduced competition level: on sites with a limiting water resource (dry climate or low WRC), foresters aim to keep the leaf area index under control, by early active logging, in order to limit water deficiency.
- Favour interspecific diversity, up to 20-30 % of beech stands. This tree diversity is considered as an insurance in case of beech decay.

Conclusion

Beech generally shows a clear response to temporal or spatial gradients, allowing modelling approaches. Simulations of beech potential situation or behaviour under future climate stimulate adaptation thinking. We suggest some focusing of scientific strength on few such cases in order to collect a critical mass of results: crossing modelling approaches, intensifying monitoring at range margin, intensifying the dialogue between science and management. The *Fagus* gender homogeneity allows sharing efforts, data and results at an international scale.

References

Dittmar, C et al. 2003 For. Ecol. and Manage. 173 : 63-78.
Badeau, V. in Loustau et al. 2004 Carbofor project's scientific report.
Bontemps, J. 2006 ENGREF PhD thesis
Jump, A.S. et al.2006 Mol. Ecol. 1-12.
Lebourgeois, F et al. 2005 Trees 19 : 385-401.
Lebourgeois F. 2006 Rev. For. Fr.
Legay, M. et Seynave 2008 8th beech symposium poster
Lousteau et al. 2004 Carbofor project's scientific report.
Penuelas, J. et Boada, M. 2003 Global Change Biology 9 : 131-140.
Seynave, I. et al., 2008 J. of Biog. (in press)

GENETIC VARIATION ON SEED STANDS OF *FAGUS CRENATA* IN NIIGATA PREFECTURE, CENTRAL JAPAN

Seiichi Kanetani*[1], Greuk Pakkad[1], Asako Matsumoto[1], Masami Tsukahara[2]
Takakatsu Hoshina[2] and Hiroshi Yoshimaru[1]

[1]Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki, Japan
Tel: + 81.29.829.8262 - Fax: + 81.29.874.3720 - E-mail address: kanekane@ffpri.affrc.go.jp
[2]Niigata Prefectural Forest Research Institute, Niigata, Japan

Introduction

To understand the genetic diversity within and among populations in a same species has been widely recognized as a key factor for the preservation of their evolutionary potential and for the utilization of human activities as logging and planting. Especially, phylogeographical information based on genetic analysis is a prerequisite for the preparation of seedling use for artificial plantation, because presence and maintenance of genetic variation are important for the long-term existence and stability in natural populations. So genetic variation can be considered as an issue in management of forest ecosystem.

Recently, in Japan, the species composition in the artificial forests consisted of even-aged monocultures species, mainly Sugi (*Cryptomeria japonica*) and Hinoki (*Chamaecyparis obtusa*), has been concerned to change and lead to mixed forests with coniferous and broad-leaved trees species. So seedlings from broad-leaved tree species have been started to nurse for plantation.

Japanese beech, *Fagus crenata*, is widely distributed throughout Hokkaido to Kagoshima prefecture in Japan. The species is a monoecious, long-lived woody angiosperm with an outcrossing breeding system by wind pollination and dominates typical cool-temperate deciduous forests. *F. crenata* plays important role as a good indicator for understanding on past forest managements in Central Japan, and seeds and seedlings of the species were started to use for undertaking to forest planting.

Niigata prefecture along the Japan Sea side is the center of the natural habitat of *F. crenata*. Beech forests in this prefecture still widely remain although they are fragmented in montane areas due to human exploitation. Local government office of Niigata prefecture established ten seed stands of the species in 2005 and has recommended to prepare autochthonous seedlings and plant it in deforested area. Therefore, it is necessary to collect and discuss the genetic information of the species. The purpose of this study is to assess the genetic diversity and differentiation in seed stands and natural forests of *F. crenata* in Niigata prefecture.

Materials and Methods

We collected 24 or 32 mature *F. crenata* trees at random from nine seed stands and three natural forests (Table 1, Fig. 1). To avoid influence of artificial plantation, the young tree with DBH < 10cm were excluded. Finally, young leaves were collected from 376 mature trees and stored at -30°C before DNA extraction. Total DNA was extracted from all samples using a modified CTAB method (Tsumura et al. 1995) and used for multiplex PCR amplification. Ten polymorphic genomic microsatellite markers that were mfc5 and mfc12 developed by Tanaka et al. (1999), and sfc7-2, sfc18, sfc36, sfc106, sfc110, sfc114, sfc195 and sfc378 developed by Asuka et al. (2004) were analysed (Table 2). Amplified fragments were detected using an ABI 3100 Genetic Analyzer and the fragment size was determined using Genotyper software ver. 3.7 (PE Applied Bio-systems).

To assess genetic diversity in 10 genomic microsatellite loci, the number of alleles per locus (*Na*), allelic richness (*Ar*), observed heterozygosity (*Ho*), expected heterozygosity (*He*) and

Wright' s fxtation index (*Fis*) in each population were calculated using FSTAT 2.9.3 software (Goudet, 1995). Genetic relationships and structure among 12 populations were evaluated by genetic distance-based PCO and neighbor joining tree, and also STRUCTURE analysis (Pritchard et al. 2000).

Result and Discussion

The ten genomic microsatellite loci were found to be highly polymorphic, with number of alleles for each locus ranging from nine (sfc195) to 38 (sfc110) . A total of 217 alleles were identified among the 376 mature *F. crenata* trees with a mean 21.7 per locus. The average number of alleles (*Na*) over the ten loci ranged from 8.5 (WD) to 12.9 (TG). Allelic richness (*Ar*) was highest in the TG and TN (11.3) and lowest in the WD (7.6). The mean expected heterozygosity (*He*) across loci per populations was 0.763, ranging from 0.683 in the WD to 0.794 in the YD. These results shows that the lowest genetic diversity was found in isolated and small population of WD where located in the northern district of Niigata prefecture.

The average inbreeding coefficient (*Fis*) ranged from -0.080 (WD) to 0.056 (TN). *Fis* values in all of the populations did not reveal significant deviation from zero. Overall population differentiation (*Fst* = 0.022) in Niigata prefecture was lower than throughout natural habitats of *F. crenata* in Japan analyzed using allozyme variation (*Gst* = 0.038; Tomaru et al., 1997). Latitudinal and longitudinal clines in allelic richness and expected heterozygosity were not found in the present study. Although significant correlations were not detected between the pair-wise *Fst* values and the geographic distance, WD and OY populations were genetically differentiated from other populations in NJ tree, PCO and STRUCTURE. These results indicate that among all seeds stands and natural forests of *F. crenata* except WD and OY in Niigata prefecture have unclear genetic structure.

Figure 1: Distribution map of sampling sites in Niigata prefecture. Black and white dots indicate seed stands and natural forests, respectively.

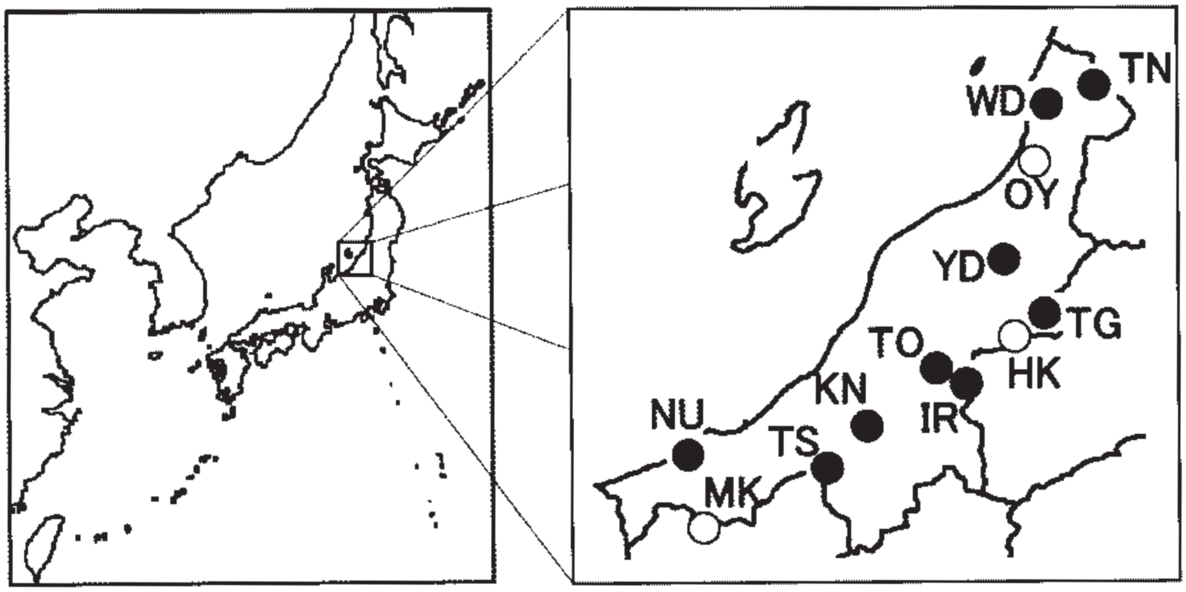


Table 1: Levels of genetic diversity within 12 populations for ten microsatellite loci.

Population	Code	Forest type	*N*	*Na*	*Ar*	*Ho*	*He*	*Fis*
Nou	NU	Seed stand	32	11.9	10.5	0.738	0.766	0.037^{NS}
Myoko	MK	Natural	32	12.3	11.0	0.724	0.766	0.055^{NS}
Tsunan	TS	Seed stand	32	12.1	10.8	0.738	0.746	0.011^{NS}
Kawanishi	KN	Seed stand	32	10.4	9.4	0.763	0.759	-0.005^{NS}
Irihirose	IR	Seed stand	32	11.4	10.3	0.773	0.757	-0.021^{NS}
Tochio	TO	Seed stand	32	11.0	10.5	0.767	0.760	-0.011^{NS}
Mikagura	HK	Natural	32	12.0	10.8	0.779	0.789	0.012^{NS}
Takigashira	TG	Seed stand	32	12.9	11.3	0.747	0.776	0.037^{NS}
Yasuda	YD	Seed stand	32	12.4	11.2	0.778	0.794	0.020^{NS}
Oshiroyama	OY	Natural	24	9.8	9.7	0.795	0.782	-0.017^{NS}
Waseda	WD	Seed stand	32	8.5	7.6	0.738	0.683	-0.080^{NS}
Takane	TN	Seed stand	32	12.6	11.3	0.739	0.783	0.056^{NS}
		Average	31.3	11.4	10.4	0.757	0.763	0.008^{NS}

N, number of tree sampled; *Na*, total number of alleles; *Ar*, allelic richness; *Ho*, observed heterozygosity; *He*, expected heterozygosity; *Fis*, Fixation index; ^{NS}not significant.
Ar based on minimum sample size of 23 diploid individuals.

References

Asuka, Y., Tani, N., Tsumura, Y., Tomaru, N. 2004. Mol. Eco. Notes 4: 101-103.
Goudet, J.1995. J. Hered. 86: 485-486.
Nagaike, T., Kamitani, T., Nakashizuka, T., 2005. Can. J. For. Res. 35: 2832-2840.
Pritchard, J.K., Stephens, M., Donnelly, P. 2000. Genetics 155: 945-959.
Tanaka, K., Tsumura, Y., Nakamura, T. 1999. Theor. Appl. Genet. 99: 11-15.
Tomaru, N., Mitsutsuji, T., Takahashi, M., Tsumura, Y., Uchida, K., Ohba, K. 1997. Heredity 78: 241-251.
Tsumura, Y., Yoshimura, K., Tomaru, N., Ohba, K. 1995. Theor. Appl. Genet. 91: 1222-1236.

RADIAL GROWTH AND DOMINANT HEIGHT GROWTH OF BEECH: SPATIAL PATTERNS AND ECOLOGICAL DETERMINISM AT THE SCALE OF FRANCE

Myriam Legay*[1], Ingrid Seynave[2] and Daniel E Silva[1]

[1] Interface Inra/ONF, UMR 1137 Ecologie Ecophysiologie Forestière,
Centre INRA de Nancy, 54 280 Champenoux, France
Tel: + 33.3.83.39.40.51 - Fax: + 33.3.83.40.22- E-mail: legay@nancy.inra.fr
[2] INRA, UMR 1092 Laboratoire des Ressources Forêt Bois, 14 rue Girardet, 54000 Nancy
Tel : +33.3.83.39.40.41 - Fax: +33.3.83.39.40.34 - E-mail : seynave@engref.fr

1. Context and objectives

The assessment of climate change impacts on tree species requires the analysis of the ecological determinism of the plants fitness components. Among these components, growth is an interesting parameter, available in forest inventory databases and of major importance for species management. Site index is a height growth index, nearly independent from silvicultural techniques and strongly correlated with total production, but defined only for pure and even-aged stands. Radial growth is easy to measure in any stand but density dependent. The spatial patterns and ecological determinism of these two components of beech growth were studied separately. Here we present the unpublished results obtained about radial growth and compare the two approaches and their results.

2. Materials and Methods

2.1. Data

To study beech radial and height growths, we used the French National Forest Inventory (IFN) database containing 97,281 localised temporary plots, distributed all over the metropolitan territory. Data were collected between 1989 and 2004. On each plot, dendrometric information was collected within a radius of 6, 9 or 15 metres radius, depending on the diameter of the stems. The diameter at breast height, the total height and the width of the last five rings (RI5) were measured for all trees. IFN ecological data included topography, soil properties (from a soil pit) and geology (from geological map). These data were evaluated on a circular plot with a radius of 15 m. To complete this data set, we used climatic variables derived from the AURELHY climatic model (Meteo France-Benichou 1987).

2.2. Modelling approaches

Radial growth is very sensitive to age and stand density. To study the link between radial growth and ecological variables, we tried to limit these impacts by taking into account only the radial growth of the dominant trees which are less sensitive to competition. By modelling their radial growth as a function of dendrometric variables, we verified that this dominant radial growth was weakly affected by density and dominant dimension of the stand.

To study the relationships between height growth and ecological variables, we used the site index (SI) that is the mean total height of the hundred largest trees per hectare at a reference age. SI is widely employed by foresters because it is very nearly independent from silvicultural techniques. But it is only defined for pure and even-aged stands. So we selected the 819 plots where (i) age measurements were performed, (ii) the within plot variation in age was less than 30 years, and (iii) more than 70% of the basal area in beech. Site index was calculated at the reference age of 100 years, using a dominant height growth model (Seynave et al 2008).

2.3. Spatial representation at the scale of France territory

To represent the spatial variability of radial growth, the territory was divided in 9,892 quadrates of 8 by 8 kilometres. A mean value of radial increment of dominant trees was calculated over each quadrate.

To map height growth, the model linking site index to ecological variables was applied to predict height growth on 97,281 IFN-plots. A kriging technique was used to interpolate estimated height growth. During a second stage, we modelled the limits of the range for beech using the all 97,281 IFN-plots where the presence or absence of beech have been observed. An indicator kriging built the isoline of frequency and we assumed as limit of range of beech, the isoline 10%.

3. Results

3.1. Radial growth model

RI0 was linked to six environmental variables by the equation 1:

$$[1]\ RI0 = 1.9 * tm5 - 1.0 * tx7 - 0.36\ pro + 0.30 * depth + 2.0\ ghum - 0.03\ E678 + 19$$

RI0 : the mean of RI5 of the dominant beech in the plot (in mm)
tm5 : minimum May temperature
tx7 : maximum July temperature
pro : proportion of rock outcrop (tenths of the plot area)
depth : soil depth
ghum : type of humus : ghum=0 in case of a mor, 1 in the other cases.
E678 : potential evapotranspiration during June, July and August (according Turc 1987)

This model explains 22 % of the variance in radial growth index.

3.2. Potential height growth model

The site index model (Seynave et al 2008) included seven environmental variables:

$$[2]\ SI = 3.9 * t5 - 2.8 * t7 - 0.3 * t1^2 - 0.57.10^{-4} * p12^2 + 0.35 * depth - 0.37 * C/N - 0.16 * pH^2 + 38.4$$

SI : site index (in m)
Climatic variables :
t5, t7, t1 : mean May, July, January temperature
p12 : total December precipitation
Soil variables :
depth : soil depth
C/N : bioindicated C/N (using the EcoPlant indicator values, Gegout 2005)
pH : bioindicated pH

This model explained 59% of the variations in site index.

4. Discussion

The comparison of the models [1] and [2] reveals that radial and height growth of beech in France share some common ecological factors: temperature in early spring (with a positive effect of minimum or mean May temperature), summer temperature (with a negative effect of July temperature and summer evapotranspiration), and depth of the soil (positive effect). The inclusion of these variables in both of the models is consistent with the ecophysiological interpretations purposed by Seynave et al. (2008): the importance of early spring that is a period characterised by a favourable water balance, and the negative effect of high

temperature in summer, leading to water deficit and stomatal closure.
The secondary climatic factors of the height growth model, January temperature and December precipitation, have a significant effect on radial growth, but they were not retained in model 2 due to their weak contribution to total variance.

Throughout France, the spatial variations in radial and height growths present similarities. In the east part of France, both decrease with the increasing latitude and the lowest growths were observed in the south of the Alps and in the south-east of the Massif Central. However, for some part of France, the geographic patterns between radial and height growth are different. As an example, the height growth model predicts a decrease of site index towards the west mainly due to high winter temperature. By contrast, in this region, the radial growth index is high.

Near the boundaries of species range, the variations in radial and height growths are similar.
In the southern half part of France, both decrease towards the south range limit of beech. This reduction in growth could explain the absence of beech in high Mediterranean region as being due to physiological constraints.
In the northern part of France, the radial and height growths does not decline near the range boundaries.

The models indicate that nutritional variables also determine radial and height growth. But the variables introduced in the models are different, making the comparison of the effect of nutritional conditions on radial growth and on height growth difficult.
The establishment of models including the same variables and the use of standardized variables should improve the comparison of the ecological determinism by comparing the values of the coefficients.

References

Benichou, P. , Lebreton, O. 1987 La Météorologie 7 :23-34
Gegout, J.C. et al. 2005 J. Veg. Sci. 16 :257-260
Seynave, I. et al. 2008 J. of Biog. (in press)
Turc, L. 1961 Ann. Agron. 12:13-49

VARIABILITY IN XYLEM CAVITATION VULNERABILITY WITHIN *FAGUS SYLVATICA* TREE SPECIES ALONG ALTITUDINAL AND GEOGRAPHIC GRADIENTS IN FRANCE

Sévérien Têtè Barigah*[1], Stépahane Herbette[2], Roland Huc[3], Michel Ducrey[3]
and Hervé Cochard[1]

[1]Unité Mixte de Recherche PIAF, INRA Clermont-Ferrand
Institut National de la Recherche Agronomique, 234, avenue du Brézet 63039 Clermont-Ferrand, France
Tel: + 33.4.73.62.44.72 - Fax: + 33.4.73.62.44.54 – E-mail : barigah@clermont.inra.fr
[2]Unité Mixte de Recherche 547, Physiologie Intégrée de l'Arbre Fruitier et Forestier,
Université Blaise Pascal, 63170 Aubière, France
[3]Unité de Recherches forestières méditerranéennes, INRA Avignon, 84000 Avignon, France

Introduction

Drought stress occurs whenever soil water drops below a threshold inducing restrictions to growth and transpiration. Reduced water availability alters both soil-root and leaf-atmosphere interfaces and threatens the integrity of the liquid phase continuum from soil to leaves. This kind of stress has consequences for physiological traits related to water movement in plants, such as stomatal behaviour (Sperry *et al.*, 1998; Bréda *et al.*, 2006), photosynthetic capacity (Brodribb & Feild, 2000), turgor loss point of leaf cells (Brodribb *et al.*, 2003), and water transport capability of the xylem (Cochard *et al.*, 1992; Tyree *et al.*, 1994; Maherali *et al.*, 2004). These traits allow environmental acclimation to be achieved in many different ways.

Currently, drought year is reported to occur about once every ten years in much of Europe (Rust & Savill, 2000). Moreover, most of the current climate projections for Central Europe predict increased temperatures by 2-4.5 °C during the course of this century (Bréda *et al.*, 2006) that are expected to cause an increase in the frequency and duration of intense summer droughts (IPCC, 2001; Bréda *et al.*, 2006). Prentice et al. 1991; Prentice 1993 and Bazzaz 1996 suggest an increasing in dominance of broad-niched, early-successional species as a result of increased climatic variability, if predictions of global warming come true. Therefore, knowledge of the factors enabling these species to occupy such variant habitats is of paramount importance. A high degree of ecological variation, i.e. a wide range of different habitats potentially occupied by a species (Bazzaz 1996), can be achieved by different means: the species can show a high degree of genetic variability, comprising genotypes especially adapted to different habitats, or the genotypes can exhibit phenotypic plasticity, coding for the ability of the individual to express different phenotypes in different environments (Gregorius and Kleinschmit 1999).

The loss of hydraulic conductivity in the xylem has been recognised as playing an important role in drought response (Tyree and Sperry 1989). Xylem cavitation under negative xylem pressure and subsequent embolism results in a conduit being unavailable for water transport, thus reducing hydraulic conductivity. Pockman and Sperry (2000) suggested that a high cavitation resistance results in a higher tolerance to water deficit, and that vulnerability to embolism formation has a significant influence on patterns of species survival and distribution within areas and during periods of water limitation. Tyree and Zimmermann, (2002) stated that a correlation certainly does exist between Ψ_{50} and sylvicultural impressions of drought tolerance of woody plants. Barigah et al (2007) and Cochard et al (2007a, b) used plant water potential at 50% loss of conductivity (Ψ_{50}) as a proxy of drought resistance in plant clones and with different plant species and have shown that xylem cavitation vulnerability is a measure of species response to reduced water availability and that, the Ψ_{50} adjustments is a reliable gauge of the occurrence of drought stress.

European beech (*Fagus sylvatica*) is one of the most important forest trees in central Europe. Beech dominates natural forests from moderate dry to moist conditions and grows on a wide range of soil types, acid or basic. It mainly develops by natural regeneration and can adapt to local climatic conditions. We, therefore, used Ψ_{50} to assess spatial variation in the drought resistance of European beech (*Fagus sylvatica*) and check for its ability to exhibit phenotypic plasticity along geographical and altitudinal gradients in France North East, Centre and South East of France.

Materials and Methods

We used a customized centrifuge 'cavitron' (Cochard et al., 2005) to carry out Ψ_{50} measurements for *Fagus sylvatica* twigs from tree populations sampled along geographical (North East, Centre and South East) and altitudinal gradients (Northern side of the Ventoux mountain) in France (Table 1) where *Fagus sylvatica* dominates natural forests from moderate dry to moist conditions.

Table 1 – Sites of the beech populations provenance

	Coordinates	Altidude (m)
Ventoux	44° 11' 06.57" N, 5° 14' 05.11" E	950
	44° 11' 02.22" N, 5° 14' 16.61" E	1100
	44° 10' 45.56" N, 5° 14' 23.09" E	1260
	44° 10' 43.28" N, 5° 14' 36.04" E	1380
	44° 10' 34.82" N, 5° 14' 39.86" E	1520
Allagnat	45° 45' N, 2° 54' E	790
Hesse	48° 40' N, 7° 03' E	330
Graoully	49° 04' N, 6° 01' E	300

Results and Discussion

We found large difference in Ψ_{50} between Northern (-3.77 MPa) and Southern (-2.40 MPa) populations (Fig.1). Populations from Centre of France showed intermediate values of Ψ_{50}, but no differences emerged from populations sampled along altitudinal gradients.

Our experiments revealed that Beech populations from the Northeast part of France are more drought resistant to cavitation that those located in the South East. Beech from the Ventoux mountain area is the least resistant. We, therefore, conclude that European Beech is able to display different degree of phenotypic plasticity along geographic zone but not along an altitudinal gradient.

References

Barigah, T.S. et al. 2007. *in* Eichhorn J., Schriftenreihe der Forstlichen Fakultät Göttingen und der Nordwestdeutschen Forstlichen Versuchsanstalt. Göttingen. ISBN 3-7939-5142-1

Bazzaz F.A., 1996 in Cambridge University Press, Cambridge.

Bréda, N. et al. 2006. Ann. For. Sci. 63:625–644.

Brodribb, T.J., Feild, T.S. 2000. Plant, Cell and Environment. 23:1381-1388.

Brodribb, T.J. et al. 2003. Plant Cell Environ. 26:443-450.

Cochard, H. et al. 2007a. Journal of Plant Physiology, 165: 976-982.

Cochard, H. et al. 2007b. Tree Physiology, 27:1761-1767.

Cochard, H. et al. 2005. *Physiologia Plantarum* 124(4): 410-418

Cochard, H. 1992. Plant Physiology. 100:205-209.

Gregorius, H.R., Kleinschmit, J.R.G., 1999. Silvae Genet, 48 (3–4): 193–199.

IPCC 2001 *in* J. McCarthy, O. Canziani, N. Leary, D. Dokken and K. White. Cambridge University Press

Maherali, H. et al. 2004. Ecology. 85:2184-2199.

Pockman, W.T., Sperry, J.S. 2000. American Journal of Botany 87: 1287–1299.

Prentice, I.C. et al. 1991. Ecology 72: 2038–2056.

Prentice, I.C. 1993. Nature, 363: 209–210.

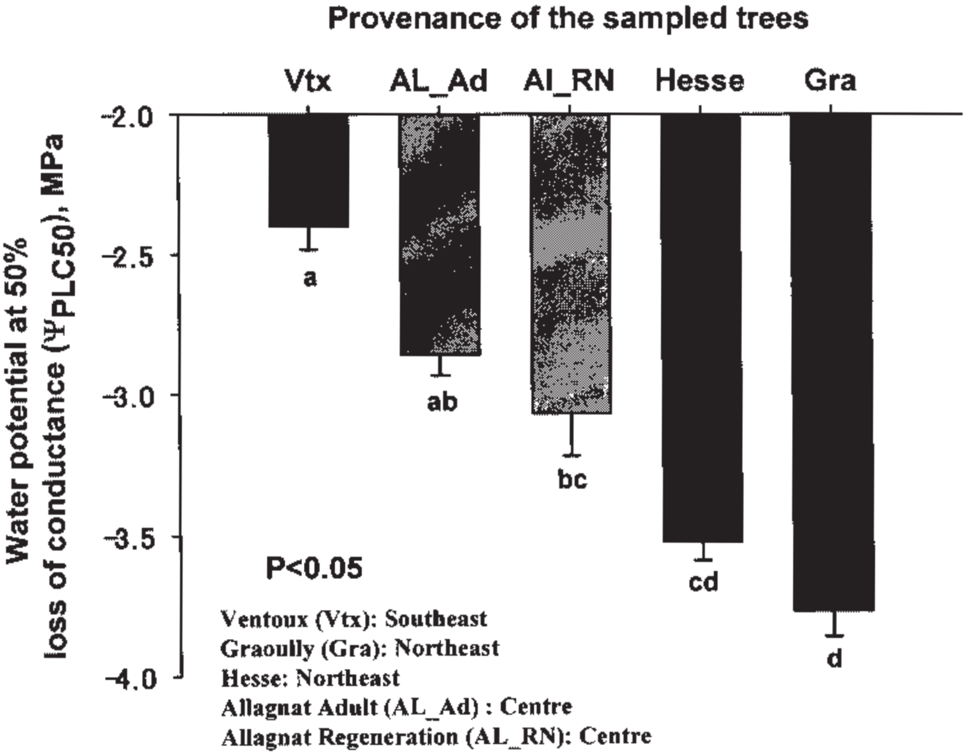
Rust, S., Savill, P.S. 2000. Forestry. 73:499-508.

Tyree, M.T., Sperry, J.S. 1989. Annual Reviews of Plant Physiology and Molecular Biology 40: 19–38.

Tyree, M.T. et al. 1994. IAWA Journal. 15:335-360.

Tyree, M.T., Zimmermann, M.H., 2002. i*n* Springer-Verlag. Springer-Verlag, Berlin, London, New York, pp. 111-168.

Figure 1: Mean xylem pressures responsible for 50% loss of conductivity among provenances of beech.



FRUCTIFICATION AND NATURAL REGENERATION OF BEECH (*FAGUS SYLVATICA* L.) ON ITS BORDER RANGE

Daniel E Silva*[1], Paola Rezende Mazella[1], Myriam Legay[1]
Emmanuel Corcket[2] and Jean-Luc Dupouey[1]

[1]Centre INRA de Nancy, 54 280 Champenoux, France
Tel: + 33.3.83.39.40.51 - Fax: + 33.3.83.39.40.22 - E-mail: esilva@nancy.inra.fr
[2]Université de Bordeaux I, 33405 Talence, France

Introduction

Beech is rarely present in the South-West of French forests. The causes are discussed: climatic limits or anthropic origins? This study aims to appreciate beech behaviour in a climate change context. If the border range of beech is climatically determined, this would imply serious risks on the species perpetuity. Thus, in this study, we have focus on plain beech, under 350 meters altitude, which represents the range of low frequencies of beech groves in France, according to the IFN data (E Silva et al., unpublished). The results of Jump et al. (2006) indicate that the decline of isolated beech populations at low altitudes is associated with global decline in mature trees. Inadequate regeneration could also be a cause of this decay. For the rest, Martinot-Lagarde (1981) indicates that natural regeneration seems to be more problematic on the plain zones. So, to better understand these problems, we have studied fructification and natural regeneration of *Fagus sylvatica* in closed populations of the South-West of France, because they are two fundamental phases for species preservation on the border ranges.
The objectives of this study are: (i) to isolate regional climatic factors and population characteristics determining the fructification of beech grove on the border range; (ii) to find which ones have an effect on density of regeneration in closed populations; (iii) to quantify fructification and regeneration correlations.

Materials and Methods

Between June and September of 2007, we have estimated beech cupules and seedlings densities (height <0.30m) in 71 populations of beech in the South-West of France. Selection of these ones has followed some criterions:

- to spread the completeness of the zone of low frequency beech groves,
- ecological factors within a site have to be homogeneous,
- beech have to be dominant in the population in proportions and status,

In each selected population, 5 circular unities of 2m² are systematically determined, at 11 meters of the site center. Dendrometrical, topographical, pedological characteristics and flora are observed in a 700m² site, including the five unities. Distance between these ones and nearer mature beech tree is recorded.
Multiple regression have been used for statistical analyses, with 8.2 version of the SAS software®. Climatic data used are means of the last thirty years, and come from AURELHY Météo France data model.

Results and Discussion

(i) Fructification:

The analysed variable is the neperian logarithm of beech cupules densities (number per meter squared) by site. Cupules densities depend on the degree of pureness of populations in beech, the variable tested is the proportion of the beech basal area comparatively to the total basal area (all tree species). This only concerns individuals with diameters greater than 7.5cm. This parameter explains 55% of the total variability ($R^2=0.55$ / $P<0.0001$) and have a positive effect on cupules densities. Acidity of soil, represented by humus, is the second local parameter contributing to the variability ($R^2=0.03$ / $P<0.0001$). It has a positive effect on the cupules densities. The linear model explains 58% of the total variability:

$$Ln_{CupDens} = 3.157 + 2.3571 \times PGoH + 0.0751 \times Humus.$$

Cupules abundance is essentially determined by the degree of pureness of beech (PGoH). It may be possible that polinisation is better in pure populations, because of the pollen flow increasing with density of the specie. Soil acidity (type of humus in our data) probably has an effect on the degradation rate of cupules which can rise to an accumulation of some years of fructification.

(ii) Regeneration:

The analysed variable is the neperian logarithm of beech seedling densities (number per meter squared) by site. Seedlings densities depend on the longitude of the site ($R^2=0.15$ / $P<0.0001$) and have a positive effect. Woody vegetation coverage explains 9% ($R^2=0.09$ / $P<0.0001$) and has a negative effect. The linear model explains 24% of the total variability:

$$Ln_{SeedlingsDens} = -0.1424 + 21\ E^{-7} \times Longitude + 0.0063 \times Cover.$$

Natural regeneration of *Fagus sylvatica* is partially determined by the climate trough a continentality gradient, represented by longitude. This factor combines several climatic parameters as minimal temperatures or annual number of frost days. There are three possible explanations:

- a positive effect of low temperatures on germination (dormancy release),
- a protection of seeds by the snow cover against predation or pathogens,
- a increase of mortality or a limitation on seedling development by drought.

These results confirm those of Buffet (1981) who points out that the success of the first phases of beech regeneration responds to a longitudinal gradient at the France scale, positive from west to east. For the rest, Oswald (in Teissier du Cros et al., 1981) indicates that probabilities of natural regeneration success are as poorer as winters are less severe.

The negative effect of vegetation coverage on cupules densities is probably due to the decreasing light quantity that it causes, light being essential for the germination and the growth of seedlings.

(iii) Relation Fructification / Regeneration:

No relation was found between cupules densities and those of seedlings. Several interpretations are possible to explain this disconnection:

- existence of a climatic filter during the transition from seed to seedling;
- variability of seed predation between sites;
- estimation of densities at different time scales (accumulation of several years of fructification and different ages of seedlings).

In conclusion, spatial variations of climate have a significant effect on seedlings densities, this could contribute to the limitation of beech in the South-West of it range. However, no clear geographical limitation appears for this phenomenon, and we have seen that local conditions could have a significant impact on the seedlings densities. Others analyses with more data would have to be lead.

Figure 1: A - Relation between cupules densities and proportion of basal area of beech; B – Relation between cupules density and acidity of soil (type of humus)

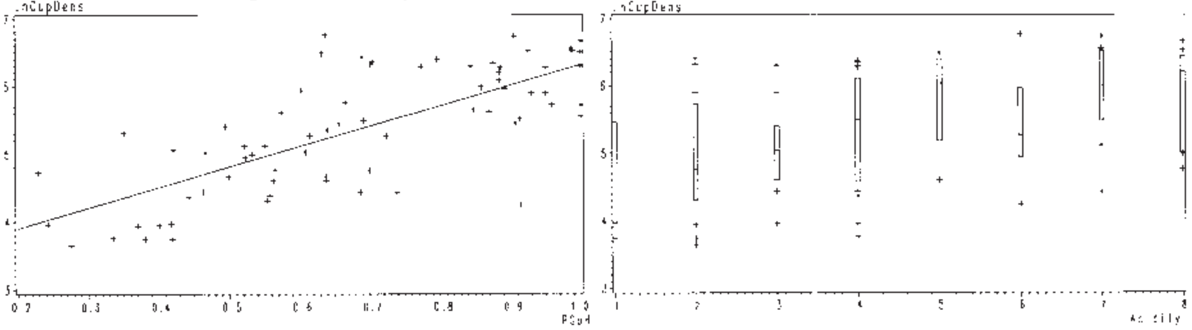
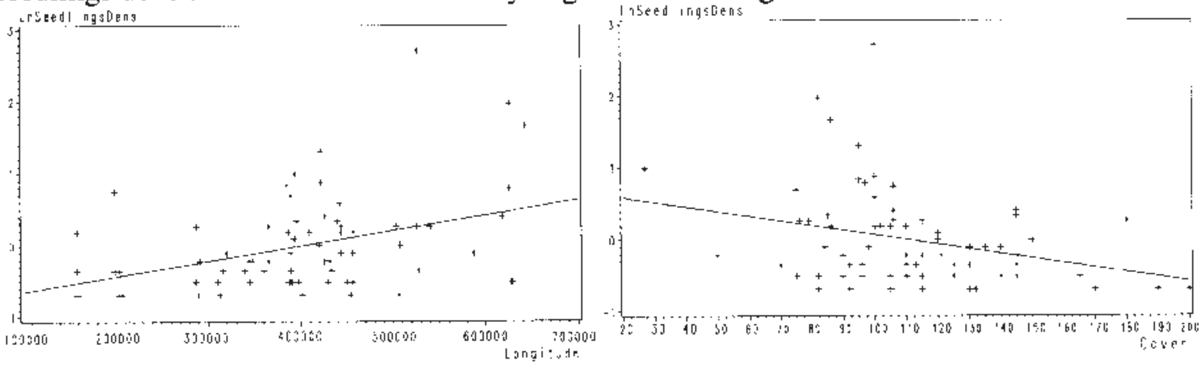


Figure 2: A - Relation between seedlings densities and longitude; B – Relation between seedlings densities and cumulated woody vegetation coverage



Abbreviations

$Ln_{CupDens}$: cupules densities neperian logarithm

$Ln_{SeedlingsDens}$: seedlings densities neperian logarithm

PGoH: proportion of beech basal area

Cover: cumulated woody vegetation coverage (height >0.30m)

References

Jump, A.S., Hunt, J.M. & Peñuelas, J. 2006. Glob. Ch Bio 12: 2163-2174.

Martinot-Lagarde, P. 1981. Rev. For. Fr. 33: 154-157.

Buffet, M. 1981. ONF Bull. Tech. n° 13: 29-47.

Teissier du Cros, E., Le Tacon, F., Nepveu, G., Pardé, J., Perrin, R., Timbal, J. 1981. (Eds.), *Le hêtre*, INRA, Paris, 377-446.

THE INTERACTION OF WATER STRESS AND SHADE DETERMINES THE PHYSIOLOGICAL RESPONSE OF SEEDLINGS TO SUMMER DROUGHT IN A MARGINAL SPANISH BEECH FOREST

T Matthew Robson*[1], Jesús Rodríguez-Calcerrada, David Sanchez, Francisco Javier Cano and Ismael Aranda

[1] Centro de investigación forestal, Instituto Nacional de Investigación Agraria y Alimentaria (CIFOR-INIA), km 7.5 Careterra a Coruña, Madrid / Unidad de Anatomía, Fisiología y Genética Forestal, Escuela Técnica Superior de Ingenieros de Montes, Universidad Politécnica de Madrid (UMP), Ciudad Universitaria s/n 28040, Madrid, Spain. Unidad Mixta INIA-UMP robson@inia.es aranda@inia.es

Introduction

In the Central Mountain range of the Iberian Peninsula scattered beech-oak forests survive at the distributional limit of beech within Europe. Summer drought is becoming more pronounced in this region, characterised by a continental climate of cold winters and hot dry summers, most precipitation falling in the early spring. The severity of drought in the Mediterranean, southern and central Europe is expected to increase under climate change scenarios. To regenerate under these conditions beech must overcome a combination of both understory shade and drought.

Late successional trees generally employ a stress-tolerant strategy of phenotypic stability and conservative resource use to counter adverse environmental conditions, but they lack the capacity capitalise on release from resource limitation (Valladares *et al.*, 2002). There is some evidence from Mediterranean forests that when combined with drought stress the facilitative effect of nurse trees on late-successional forest species in reducing the radiation load and direct drying effect of solar radiation is outweighed by the competition for soil moisture and interception of precipitation imposed by mature canopy trees (Aranda *et al.*, 2002).

In understory shade, seedlings must maximise light capture to maintain a positive carbon balance through photosynthesis, but this precludes stomatal closure to conserve water under drought stress (*sensu. the trade-off hypothesis*; Smith and Huston, 1989). Furthermore, hydraulic architecture acclimated to shaded conditions also often leads to low uptake and inefficient movement of water through the plant resulting in an additive relationship between drought and shade stresses. In forest gaps, high light levels and large vapour pressure deficits (VPD) hinder water retention and might suggest a synergistic relationship between gradients of increasing drought and sunlight (*sensu.* Sack and Grub, 2002). However, seedlings in a gap may have recourse to more physiological mechanisms than those in the understory as means to regulate water loss or a greater capacity for osmotic adjustment (Aranda *et al.* 2001). Likewise the biomass allocation of trees under shaded conditions may also be contrary to that under water stress (Veneklaas and Poorter, 1998).

Although some controlled nursery studies support the idea that acclimation to shade constrains seedlings response to drought for selected physiological variables (Aranda *et al.* 2005), others have not found evidence for a shade-drought trade-off in terms of survival and growth (Sánchez-Gómez *et al.* 2006). Likewise, inter-annual comparisons of understory natural regeneration have been inconclusive (Sack and Grubb, 2002).

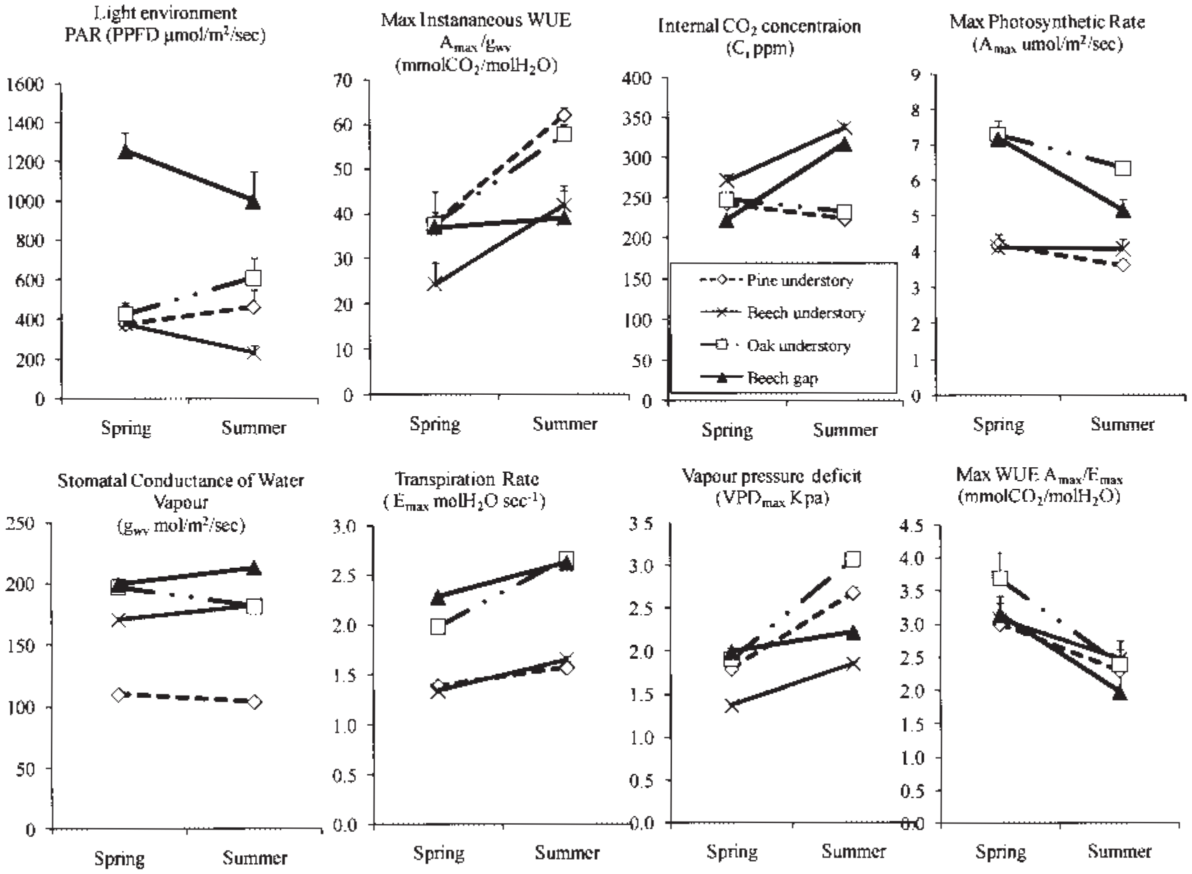
Materials and Methods

The interactions of shade and drought were studied in the *Hayedo de Montejo:* A semi-natural mixed temperate forest of particular conservation and biodiversity value within the

UNESCO World Biosphere reserve *Cuenca alta del Rio Jarama.* Beech co-exists in mixed stands throughout these forests in a hierarchy of mid-late successional trees: with *Quercus petraea, Quercus pyreniaca, Fagus sylvatica, Ilex aquifolium,* (in order of increasing shade tolerance).

The performance of beech seedlings growing under a gradient of intensities of light in forest gaps and the under oak, beech, and pine trees was compared in spring when water stress was relatively mild and in late summer under severe drought conditions. The plasticity of morphological and physiological leaf traits in response to these stresses was assessed.

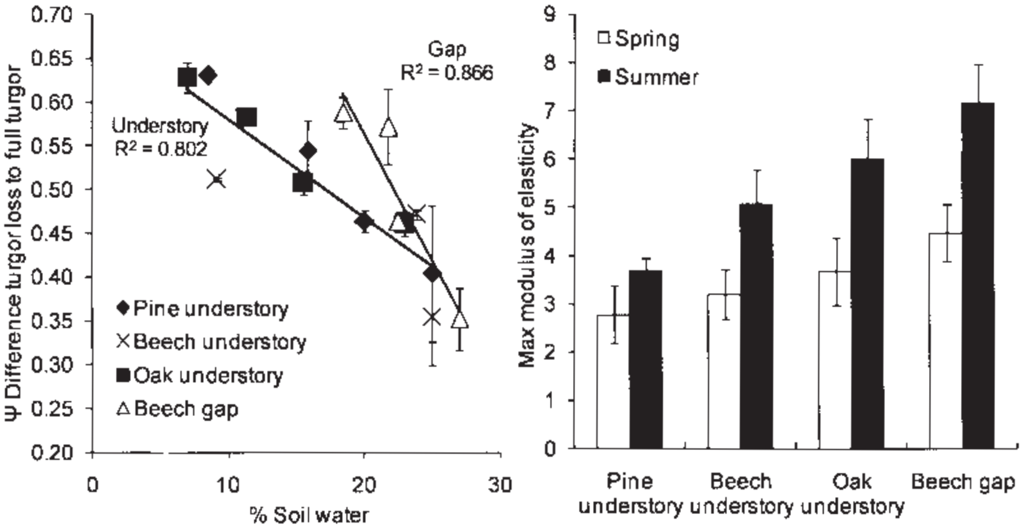
Figure 1: Changes in climatic variables and leaf physiological traits from spring to summer drought in beech seedlings under four contrasting forest environments.



Results and Discussion

In the spring, beech seedling in the gap grew best and demonstrated the most favourable physiological traits, photosynthesis and water use efficiency. However during the summer drought those seedlings developing in moderate shade under an oak canopy attained the highest photosynthetic rate and high water use efficiencies (instantaneous and intrinsic) despite high vapour pressure deficits. Those beech seedlings growing under the denser beech and pine understories suffered the largest decreases in water use efficiency from spring to summer. The advantage of understory shade during the summer drought was insufficient to offset the greater photosynthetic rates of the gap seedlings in the spring, which allowed them to develop early and attain greater plasticity in their physiological drought avoidance mechanisms.

Figure 2: a) The capacity of seedlings to accumulate solutes effecting leaf water potential in gaps is greater than the understory. b) The modulus of elasticity at maximum turgor increases along a gradient from deep shade to a gap. These differences becomes more defined as summer drought intensifies.



Shade: Although shade tolerant, beech seedlings in *Montejo* regenerating under pine responded positively to thinning, which produced an increase in daily mean summer photosynthetic photo flux density from 646 to 1227 mol.m^{-2}. In this respect, the shade tolerance of beech is less extreme than for example of holly in the same stand (Aranda *et al.*, 2008).

Rapid acclimation and a consequent growth spurt occurred in response to partial gap opening up to 40% of full sun light (equivalent to a small gap). However, the canopy composition as well as light penetration are important in calculating the extent of soil drying. Seedlings grew better under oak than under pine because of the more conservative water use by mature oak than pine trees allowed the soil to remain moist for longer (Aranda *et al.*, 2002).

Drought: Low Ψpd (correlated with soil water limitation), is ever-present during summer drought, as expected in a Mediterranean climate (Aranda *et al.*, 2000). Osmoregulatory drought-avoidance responses in beech involve stomatal control of water loss, osmotic adjustment, and restriction of hydraulic conductance.

Stomatal closure in beech is tightly correlated with vapour pressure deficit under water stressed conditions, and as such is an importance drought avoidance response (Aranda *et al.*, 2000). However it is a better strategy against acute intermittent water stress than prolonged drought because it does not allow the leaf to maintain physiological activity.

References

Aranda I *et al.*, 2000 *Trees* 14, 344-352.
Aranda I *et al.*, 2001 *Trees* 15, 358-364.
Aranda I *et al.*, 2002 *Forest Ecology and Management*, 162, 153-164.
Aranda I *et al.*, 2005 *Plant Ecology*, 179, 155-167
Aranda I *et al.*, 2008 *Trees* 22 375-384.
Sack L Grubb P, 2002 *Oecologia*,131 175-185.
Sánchez-Gomez D *et al.*, 2006 *Tree Physiology*, 26 1425-1433.
Smith T Huston M. 1989 *Vegetatio*, 83 49-69.
Valladares F 2002. *Trees* 16 395-403.

FOREST ATTRIBUTES CONTRIBUTING TO THE EXPANSION OF SIEBOLD'S BEECH POPULATION AT ITS NORTHERN DISTRIBUTION FRONT

Makoto Kobayashi*[1], Tetsuya Matsui[2], Kunikichi Yoshida[3] and Takashi Kohyama[1]

[1] Graduate School of Environmental Earth Science, Hokkaido University
Tel: + 81.11.706.2264 - Fax: + 81.11.706.4954 - E-mail: kobayan@ees.hokudai.ac.jp
[2] Hokkaido Research Station, Forestry and Forest Products Research Institute
[3] Memuro town

Introduction

Siebold's beech (*Fagus crenata* Blume) is one of the widely distributed representative canopy tree species in cool-temperate forests of Japan. The northern distribution front of beech is located at the Kuromatsunai Depression, Oshima Peninsula in southwestern Hokkaido (Tatewaki 1958a). This area forms the boundary between cool-temperate forests dominated by beech and pan-mixed forests consisting of deciduous hardwood species, with evergreen coniferous species (Tatewaki 1958a). Palynological studies indicate that beech forests began to extend its range northward after the last glacial period at apporoximately 12,000 yr B.P., expanding its range at the present northern front by about 1,000 yr B.P. (Igarashi 1994, Kito 2003). Matsui et al. (2004) predict northeastward shift of potential beech forest distribution in Hokkaido, and suggest that beech forests are able to expand its present range further towards northeast of the island.

Distribution pattern and community dynamics of beech in the distribution front suggest functional factors for the invasion, domination and expansion process of beech populations in its distribution front. There are a small number of studies of invasion mechanisms and forest dynamics in the distribution front at a scale of community and population. The movement of the boundary is the result of community dynamics played by invading species and resident species. To understand the boundary dynamics, it is necessity to demonstrate population processes of beech and to specify functional factors, which contribute to the dominance of beech population in its range boundary region. In this region we examined: (1) geographic transition of forest structure with beech and characteristics of invaded forest patches by beech in its distribution front, (2) the appearance of regeneration safe-site and growth performance of beech in relation to non-beech species, and (3) specific hervibours exhibiting severe pressure on beech and their restrictions in the northern front beech forest.

Materials and Methods

This study was conducted at the northern distribution limit area of beech forest and at adjacent beech-absent area (Fig. 1). We established study plots in the forests of which edaphic and artific factors were less severe (Fig. 1). In each study sites, we established 114 plots (including literature data (Tatewaki 1958b)) and measured the diameter at the breast-height (DBH) of all the tree species over 2 m in height, and calculated the Shannon-Wiener's index (H'), based on the total basal area (BA) of each tree species.

In addition, we established survey plots in the northernmost beech forest in Tsubamenosawa (Fig. 1), to clarify the survival process of the beech seedlings. We have censused the demography of current-year seedlings (germinated in 2003) for the two consecutive years. Generalized linear model (GLM) with the parameter selection by AIC were performed to explain the mortality of the seedlings. In this site, we also measured: (1) shoot growth increment of beech saplings, that were less than 2 m tall for the past five consecutive years, (2) seedling density of beech less than 50 cm tall, and (3) specific leaf area (SLA) of each leaf of the beech saplings less than 2 m tall underneath three canopy types (beech, *Quercus crispula* and gap) before the canopy closure in 2007, (4) photon flux density at 1-h interval at 2 m above the ground under the five different canopy types (beech, *Quercus crispula*, *Tilia japonica, Magnolia obovata* and gap) from 13 May to 14 July in 2007. Moreover, we investigated leaf phenology of six canopy species from 2005 to 2008: beech (*Fagus crenata*), oak (*Quercus crispula*), *Magnolia obovata, Acer mono, Tilia japonica* and *Betura ermanii*.

We collected leaf herbibours (arboreal caterpillars) on beech trees in the beech forests, both in the continuous and isolated beech forest areas in 2005 and 2006.

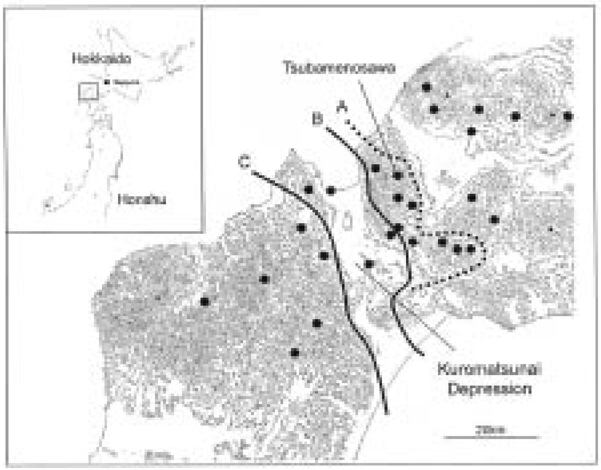


Figure 1: Study sites (●) and northern distribution front area of *Fagus crenata* in Hokkaido, northern Japan. Line A: the natural distribution front by scattered stand with mixture of beech trees. Line B: the distribution front of beech-dominated forests (Kito 2003). Line C: the distribution front of continuous beech-dominated forests (Kito 2003).

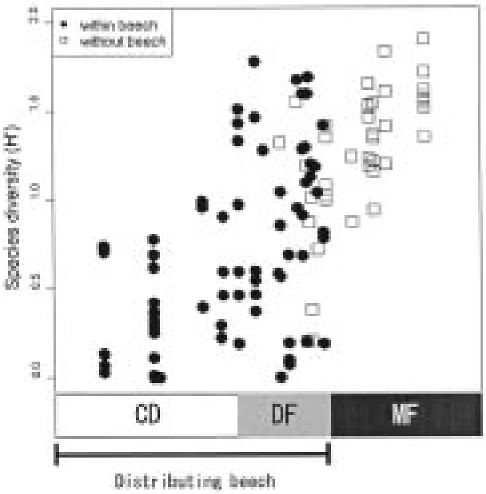


Figure 2: Geographic transition of tree species diversity along the boundary.
CD: continuous distribution area of beech forest. DF: distribution front of beech. MF: deciduous mixed forest without beech.

Results and Discussion

The changes in Shannon-Wiener's index were found from southwest to northeast (Fig. 2). This geographical pattern of species diversity suggests that decrease in species diversity with beech invasion in the distribution front. The probability that a beech tree was surrounded by other beech trees, was lower in the front populations than in the populations in the continuous beech forests. Therefore, interspecific interaction was important for the beech invasion and establishment into the northern non-beech forests.

Onset of the bud burst for beech was earlier than that of other canopy species, and the speed of leaf expansion was rapid. The bud burst for the representative dominant oak in the mixed forest was about 2 weeks later than beech. The light conditions under the canopy before leaf flush did not show much differences among the four canopy species (Fig. 3). It began to decrease the light attenuation under the beech crown in proportion to leafing phenology. Light condition was good under the canopy of oak and *Magnolia obovata* before their leafing but after the light perfectly attenuates under the beech canopy. Therefore, the seasonal gap appeared under the canopy of oak and *Magnolia obovata*. It was dark under the beech canopy after the light attenuates, and it was light under the canopy of oak and *M. Obovata*.

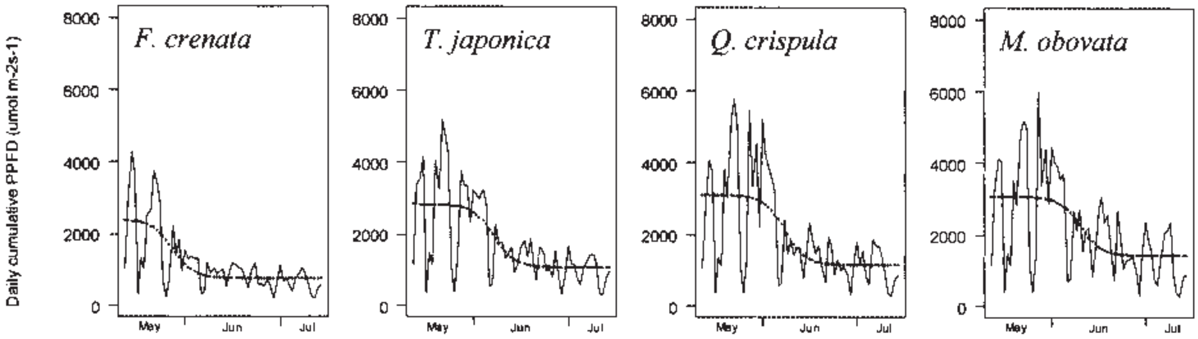


Figure 3: Changes in the daily cumulative PPFD under canopies of four species (*F. crenata, T. japonica, Q. crispula* and *M. obovata*) during the 13 May to 14 July. Dotted line indicates logistic curve fitting.

The density of beech seedlings did not show significant diferences among the three canopy types ($p>0.05$). However, the plot, under which most beech seedlings appeared, was under the oak canopy (52 individuals per 16 m^2). The shoot growth of beech saplings for the last 5 years under the beech canopy types was significantly smaller than those under the oak and gap canopy types ($p<0.05$). SLA of beech saplings under the different canopy types before canopy closure was different ($p<0.05$). The survival rate of beech seedlings during the first and the second year was 23.7% and 4.8%, respectively. GLM analysis found that two parameters significantly contributed to the mortality of the first-year beech seedlings: (1) the cover of beech canopy and (2) the density of dwarf bamboo. Contributing factors to the GLM for the mortality of second-year beech seedlings were: (1) precent coverage by other canopy species and (2) germination density of beech seedlings in the first year. The parameters of beech canopy coverage for the first year and the coverage of other canopy species canopy were significantl ($p<0.05$ and $p<0.01$, respectively).

In this region, four species of specialist herbivours (arboreal caterpillars) for beech were identified; however only one species (*Catocala nubila* Butler) appeared in the distribution front. In addition, the specialist herbivour, which gives the severe predation pressure on beech, *Syntypistis punctatella* (e.g. Kamata 2000) was restricted to the beech continuous range.

These results indicate that the tree community structure in the distribution front provides safe-sites for beech invasion and establishment, and that the beech trees have high growth performance. In addition, beech population can be escaped from the severe pressures by specific hervibours. Therefore, community structure in the distribution front positively contributes to the proccess of beech population expansion.

References

Tatewaki, M. 1958a. J. Fac. Agric. Hokkaido Univ. 50: 271-486 (in Japanese with English abstract).
Tatewaki, M. 1958b. Hakodate forest office (in Japanese).
Igarashi, Y. 1994. Forest Tree Breeding of Hokkaido 37:1-7 (in Japanese).
Kito, N. 2003. Shinrin Kagaku 37:46-50 (in Japanese).
Matsui et al. 2004. Journal of Vegetation Science. 15: 605-614.
Kamata, N. 2000. Population Ecology. 42: 267-278.

DEVELOPING THE DISTRIBUTION MODEL OF *FAGUS CRENATA* FOREST FOR LOCAL LANDSCAPE MANAGEMENT USING CLIMATIC, TOPOGRAPHIC AND HUMAN DISTURBANCE FACTORS

Yasushi Mitsuda*[1] , Toshiro Iehara[1], Makoto Sano[1] and Hiroshi Tanaka[2]

[1]Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki, Japan
Tel: +81-29-829-8313 - Fax: +81-29-873-3720 - E-mail: mitsuda@ffpri.affrc.go.jp
[2]Kyushu Research Center, Forestry and Forest Products Research Institute, Kumamoto, Japan

Introduction

In Japanese cool-temperate mountainous regions, local broad-leaf forests are often either Buna (*Fagus crenata* Blume) forest or Mizunara (*Quercus mongolica* Fisch. ex Turcz. var. *crispula* (Blume) Ohashi) forest, due to the difference of their suitability for environmental gradients. The spatial distribution of suitable habitat for both indigenous tree species is essential to manage the local forest landscape. Matsui et al. (2004) developed a model of the distribution of *F. crenata* at a national scale using 1-km resolution climatic factors. Referring to their model, we attempted to model the spatial distribution of the suitable habitat of *F. crenata* at the local scale.

Several studies have revealed that environmental gradients derived from topography also regulated the distribution of tree species at the local scale as well as climatic factors (e.g. Guisan and Zimmermann, 2000). Readily obtainable climate data has coarser resolution than data of a meaningful resolution to represent topographic effects on tree species distribution. This causes spatial misalignment and hinders statistical analysis (Gelfand et al., 2006). Human intervention in natural forests also makes it difficult to reveal the true relationship between species distribution and environmental factors (Gelfand et al., 2006). Recently, the Markov Chain Monte Carlo (MCMC) method which can deal with these two problems has been developed. Thus, the objective of this study is to develop a model of the distribution of *F. crenata* forest at the local scale using climatic, topographic and human disturbance factors.

Materials and Methods

This study was conducted in Takahagi and Kitaibaraki City, Ibaraki Prefecture, Japan, where much of the forested area has been converted to Sugi (*Cryptomeria japonica* D.Don) or Hinoki (*Chamaecyparis obtusa* Endl.) plantations. Furthermore, many of the remaining natural forests were subject to human use such as removal of wood for fuel.

A land-cover map of the area was made from aerial photographs. This map contains the class of forest vegetation in which we are interested, namely *F. crenata* forest and other deciduous broad-leaf forests where mainly *Q. mongolica* var. *crispula* dominates. The 50-m resolution digital elevation model (DEM) published by the Japanese Geographical Survey Institute was used to represent topographic features. Mesh Climatic Data 2000 published by the Japan Meteorological Agency, which contains 1-km resolution average climatic data for the period 1971 to 2000, was used as the climatic database.

Because we used these data of different resolutions, we adopted a hierarchical model to overcome the problem of spatial misalignment as follows (Fig.1). First, we set sample points located at the center of each 50-m cell, and investigated the type of vegetation by refereeing to the land-cover map. We used F_j to represent the type of forest existing at sample point j, *F. crenata* forest or other deciduous broad-leaf forest (1 / 0). We summed up F_j over the number of sample points in 1-km cell i (N_i), to obtain1-km cell level counts NF_i. We assumed that NF_i is distributed binomially with probability PF_j and number of trials N_i.

[1] $$NF_i \sim \text{Binomial}(PF_i, N_i)$$

The probability PF_j that *F. crenata* forest existed in 1-km cell i was related to climatic factors.

[2] $$\text{logit}(PF_i) = \boldsymbol{W}_i'\boldsymbol{\alpha} + \rho_i + r_i$$

where $\boldsymbol{W}_i$ is a vector of climatic factors associated with 1-km cell i, $\boldsymbol{\alpha}$ is a vector of the associated coefficients including the intercept term for regression, ρ_i is a spatial random effect assigned by the conditional auto regressive (CAR) model and r_i is a non-spatial random effect.

At the 50-m cell level, F_j could be regarded as a random variable derived from Bernoulli trial with probability p_j.

[3] $$F_j \sim \text{Bernoulli}(p_j)$$

It is suspected that some other deciduous broad-leaf forest becomes established as substitute vegetation after human disturbance. Therefore we assumed that the probability of existence of *F. crenata* at the current state, p_j, is the joint probability of the probability of potential existence, pf_j, and the probability of undisturbed forest, $(1\text{-}ph_j)$.

[4] $$p_j = pf_j(1 - ph_j)$$

The probability pf_j that *F. crenata* forest exists in 50-m cell j is related to topographic factors and also climatic factors of that 1-km cell i that includes 50-m cell j.

[5] $$\text{logit}(pf_j) = \boldsymbol{W}_i'\boldsymbol{\alpha} + \boldsymbol{w}_j'\boldsymbol{\beta}$$

where $\boldsymbol{w}_j$ is a vector of topographic factors associated with 50-m cell j, and $\boldsymbol{\beta}$ is a vector of the associated coefficients.

Also, the probability of human disturbance is related to explanatory variables which include topographic factors and land-use factors.

[6] $$\text{logit}(ph_j) = \boldsymbol{v}_j'\boldsymbol{\gamma}$$

Here $\boldsymbol{v}_j$ is a vector of explanatory variables associated with 50-m cell j, and $\boldsymbol{\gamma}$ is a vector of the associated coefficients.

We used the MCMC method for fitting this complex model using WinBUGS.

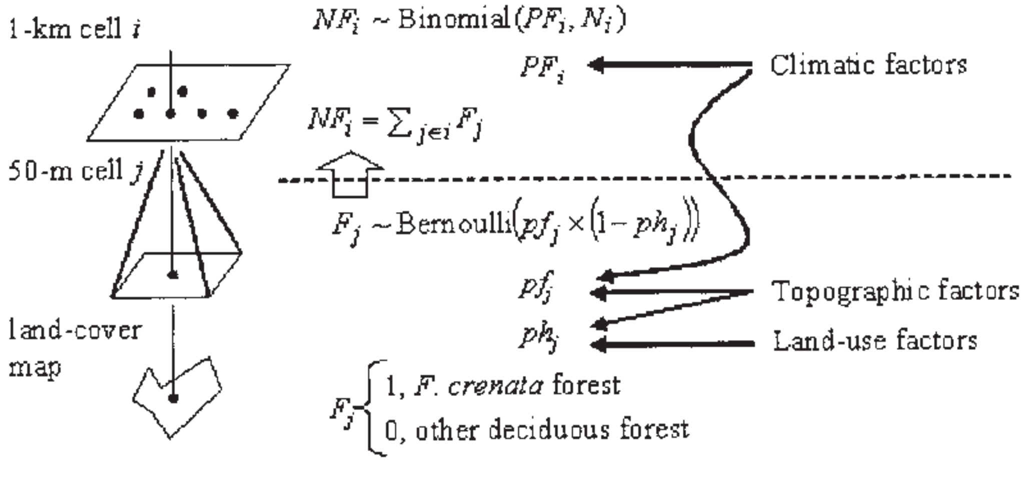


Figure 1: Illustration of the hierarchical model.

Results and Discussion

Through exploratory analysis, we developed a model of the distribution of *F. crenata* at the local scale. All explanatory variables and associated coefficients are shown in Table 1. Coldness index (CI) and winter (December-March) precipitation (PRW) were used as 1-km resolution climatic factors. Their coefficients showed that the suitable habitat for *F. crenata* was cooler and higher PRW, which meant a more snowy area. Solar radiation index calculated during summer (May-September) (SRIS) was used as a 50-m resolution topographic factor and its coefficient indicated that a site with higher SRIS, which could be a cause of water shortage, was not suitable for *F. crenata*. Previous studies (Yagihashi et al., 2003; Matsui et al., 2004) discussed the distribution of *F. crenata* in relation with water stress during summer and snow cover represented by 1-km resolution climatic data. Our results showed the similar habitat trait of *F. crenata*.

The probability model of human disturbance adopted the proportion of plantation forest area to all land-use area within the surrounding 1-km^2 square (%PLN) and elevation (ELV) as explanatory variables. Our model suggests that deciduous broad-leaf forest located in lower areas and surrounded by plantation forest tends to be disturbed by human activity.

Thus, we successfully developed a reliable and useful model to describe the spatial distribution of *F. crenata* for local landscape management.

Table 1: Statistics of regression coefficients.

	25%	Median	75%
1-km resolution			
F. crenata distribution model			
CI	-3.73	-3.42	-3.17
PRW	1.33	1.46	1.65
50-m resolution			
F. crenata distribution model			
SRIS	-0.54	-0.40	-0.28
Human disturbance model			
%PLN	1.32	1.46	1.62
ELV	-0.61	-0.48	-0.36

References

Gelfand, A.E. et al. 2006. in Clark, J.S. and Gelfand, A.E., Oxford University Press: 77-97.
Guisan, A. and Zimmermann, N.E. 2000. Ecol. Model. 135: 147-186.
Matsui, T. et al. 2004. J. Veg. Sci. 15: 57-66.
Yagihashi, T. et al. 2003. Jpn. J. Ecology 53: 85-94.

SPATIOTEMPORAL DYNAMICS OF EUROPEAN BEECH (*FAGUS SYLVATICA* L.) POPULATION IN THE PERIOD 1970-2005

Ales Poljanec[2], Andrej Ficko[2], Matija Klopcic[2] and Andrej Boncina*[1]

[1] University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable
Forest Resources, Vecna pot 83, 1000 Ljubljana, Slovenia E-mail: andrej.boncina@bf.uni-lj.si
phone: +386 1 423 11 61 fax: +386 1 257 11 69
[2] University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable
Forest Resources

Introduction

European beech (*Fagus sylvatica L.*) forests represent the most important forest communities in natural forested landscape in Slovenia. Beech has been continuously present in Slovenia since the last glacial (Sercelj 1996, Magri 2008). In the post-glacial beech expanded and became the most widely-spread tree species in Slovenia; it can be found on 89 % of total forest area, presenting 32 % of total growing stock. The contemporary distribution and structure of beech forests is the result of environmental factors (i.e. climatic conditions, site characteristics) and long history of human activities. In the 17th, 18th and 19th century decline of beech was associated with intensive harvesting of beech for iron industry; during the 19th century and in the first half of 20th century spruce was favoured in beech forests due to economic reasons (Veber 1986). In the last few decades close-to-nature forestry has been widely accepted and practiced (Mlinsek 1968); it promotes natural tree species composition and thus influences the expansion of beech and its increase in total growing stock of forest stands. The aim of the research is 1) to present characteristics of present distribution and population structure of beech in Slovenian forests and 2) to analyse spatiotemporal dynamics of beech in the period 1970-2005 by studying its spatial expansion and its increase in total growing stock of forest stands and identifying the main driving factors.

Materials and Methods

The research is based on the spatial information system Silva-SI, which covers the entire territory of Slovenia (1,140,000 ha) and includes 32,564 compartments with a mean compartment size of 35 ha. For each compartment selected data on forest resources (growing stock, increment, diameter structure, and species composition), environmental conditions (topography, site conditions, climate parameters), socio-economic conditions (ownership, holding size of forest property, land use in the neighbourhood) and forest management (annual cut, forest management region) were collected.

Influence of various predictors on spatiotemporal dynamics of beech was investigated by use of multiple regression approach. Interspecific covariation of beech with other tree species was determined with different indices, as proposed by Goodall (1973). The influence of one accompanying tree species to another in beech forests was studied by using Spearman correlation coefficient between ranks of quantity indices (QI_x), which was calculated as a portion between growing stock of tree species x and growing stock of beech. Logistic regression was used to analyze present distribution of beech and its expansion in the period 1970-2005. The increase of beech growing stock was modelled by using the general linear model, where index between growing stock of beech for year 2005 and 1970 (I_beech) was used as a dependant variable.

Results and Discussion

Present distribution and structure of European beech population

Broad ecological niche enables beech to intersperse with almost all tree species. The analysis of inter-specific relationships of beech shows that spruce, sycamore and sessile oak are the most frequent tree species associated with beech. In beech forests the strongest positive correlation was determined between sessile oak and hornbeam (Spearman's rho = 0,596), while the strongest negative correlation was found between silver fir and sessile oak (Spearman's rho = -0,359), which indicates strong site stratification of beech forests.

Present density of beech stands (share in total growing stock > 50 %) is 580 stems ha^{-1}, totalling in basal area of 29.67 $m^2 ha^{-1}$ and growing stock of 312 $m^3 ha^{-1}$. Population of beech is younger if compared to the population of spruce, and much younger than silver fir population. In beech population only 14 % of growing stock is represented in diameter class above 50 cm, whereas in spruce and silver fir population the share reaches up to 21 % and 36 %, respectively. This indicates further increase of beech portion in forest stands in Slovenia.

Dynamics of European beech population in the period 1970-2005

The area covered by beech has expanded in the period from 1970-2005, covering additional 6 % of total forest area (Fig. 1). Logistic regression model proved that environmental factors and initial stand parameters are the best predictors of spatial expansion of beech. The expansion of beech occurred more frequently on acidic bedrock, in areas with diverse topography, and areas with lower average annual temperatures. Furthermore, the appearance of beech was more frequent in areas with higher share of conifers in total growing stock, and stands with lower growing stock with small amount or even absence of large diameter trees (> 50 cm). One of the important stand predictors for beech appearance in the studied period was the distance to the nearest location where beech was present.

During the period 1970-2005 growing stock of beech almost doubled (I_beech=1.93) and its share in total growing stock of forest stands increased from 27 % to 32 %. The regression model indicates that the increase of growing stock in the period 1970–2005 was mostly influenced by forest management (harvest intensity, management regions) and different initial conditions of forest stands in 1970.

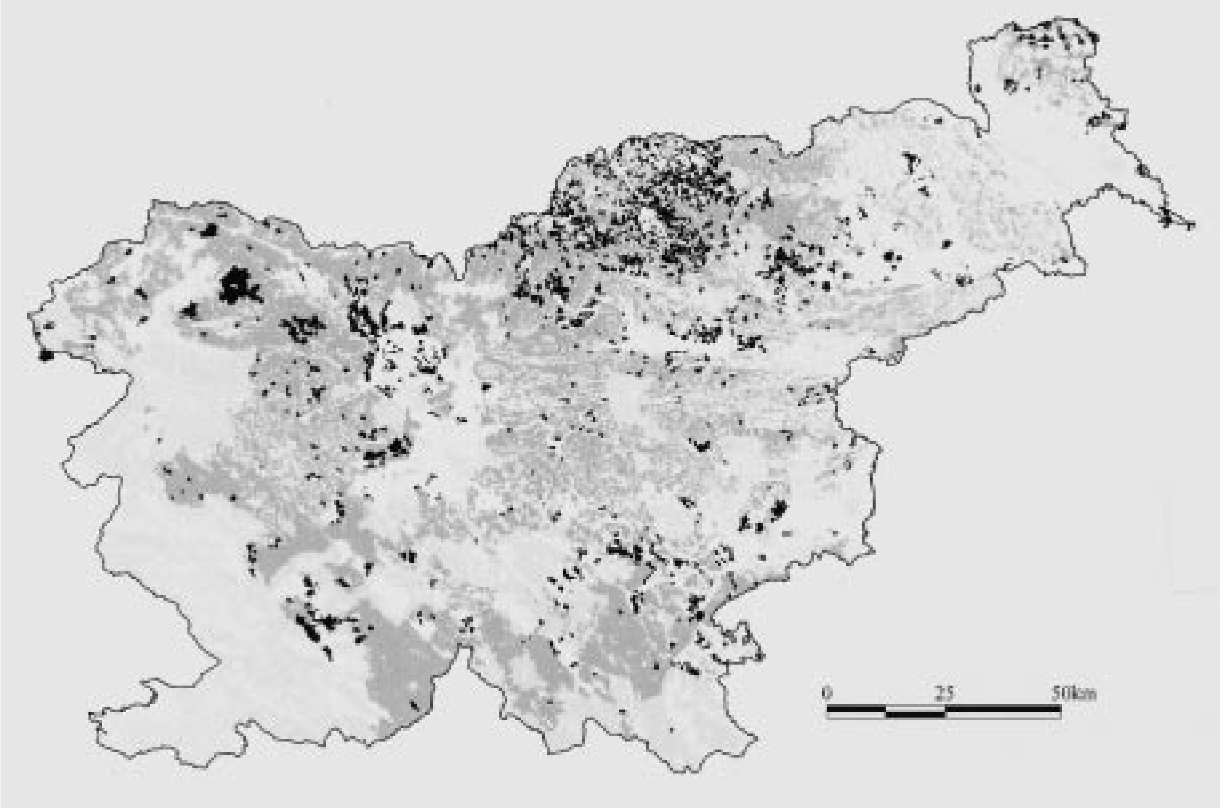


Figure 1: Spatial distribution of beech in Slovenian forests in year 1970 and its expansion in the period 1970-2005; light grey – forest stands without beech, dark grey – forest stands with beech, black – appearance of beech in the period 1970-2005.

References

Goodall, D.W. 1973. *in* Whittaker R.H., Handbook of vegetation science, 5: 557-618
Magri, D. 2008. J. Biogeogr. 35: 450-463
Mlinsek, D. 1968. Poslovno združenje gozdnogospodarskih organizacij: 117
Sercelj, A. 1996. Academia scientiarum et artium Slovenica, 35: 142
Veber, I. 1986. Gozdno gospodarstvo Bled: 48