

Quaternary International 101-102 (2003) 67-73



Pliocene and Pleistocene exhumation and uplift of two key areas of the Northern Apennines

M.L. Balestrieri^{a,*}, M. Bernet^b, M.T. Brandon^b, V. Picotti^c, P. Reiners^b, M. Zattin^c

^a C.N.R., Istituto di Geoscienze e Georisorse, Via G. Moruzzi, 1, 56124 Pisa, Italy

^b Department of Geology and Geophysics, Yale University, P.O. Box 208109, New Haven, CT, USA

^cDip. di Scienze della Terra e Geologico-Ambientali, Università di Bologna, Via Zamboni 67, 40126, Bologna, Italy

Abstract

Application of different thermochronological methods to two areas of pronounced relief (Apuane Alps and Mt. Falterona) of the Northern Apennines chain documents an average exhumation rate of about 0.7 mm/yr. This result suggests that the general exhumation of the chain is driven mainly by erosion. Nevertheless, the long-term exhumation trend seems to be perturbed by short-term events at higher exhumation rates. The time of increased exhumation rates coincides with onset of intramontane sedimentation, documenting a contribution of tectonics (local normal faulting?) to the surface uplift. The data indicate an eastward shifting of the onset of topographic relief, Early Pliocene in the Apuane Alps and Early Pleistocene in the Mt. Falterona area. © 2002 Elsevier Science Ltd and INQUA. All rights reserved.

1. Introduction

The relationship between late orogenic extension and relief evolution have been studied in several orogenic belts, but no univocal models have been provided, owing to the different geodynamic scenarios and lithospheric configurations (e.g. Basin and Range and Western Greece: Leeder and Jackson (1993), Tibet: Masek et al. (1994), Apennines and Tyrrhenian Sea: D'Agostino et al. (2001)). The eastward propagation of normal faulting in the Northern Apennines is well established (Elter et al., 1975; Bartole, 1995; Cavinato and De Celles, 1999) following the Late Neogene retreat of the lower (Adriatic) plate (Malinverno and Ryan, 1986; Royden, 1993). This history has been reconstructed essentially using the record of the sedimentary infilling of the normal fault bounded basins (Bartolini, 2003; for a review see Martini et al., 2001). Reconstructing the relief evolution in terms of uplift requires a more integrated approach, where surface processes can be linked with the exhumation of rocks derived by low-temperature thermochronological data. In this way, a quantification of the long-term trends in surface uplift and erosion can be provided, with basin stratigraphy providing independent time constraints and further paleogeographic information.

Low-temperature thermochronological systems are ideally suited for reconstructing thermal histories of rocks in the uppermost part of the crust because they record time and rates of cooling related to exhumation. Presently, a rather extensive apatite fission-track (AFT) database exists across the Apennine chain (Abbate et al., 1994, 1999), giving information about the times and the rates at which rocks cooled below the 110°C isotherm. In this work, we combine pre-existing AFT data with new zircon fission-track (ZFT) and U-Th/He analyses on apatite (AHe) and zircon (ZHe) to investigate a range of temperatures from ca. 240°C to 70°C. In order to assess the relationships between exhumation and surface uplift these methods have been applied on samples from two areas of pronounced relief, the Apuane Alps and Mt. Falterona. The data are integrated with information gained from the sedimentary record of adjacent basins. The reconstructed uplift history will allow a better comprehension of the geomorphic equilibrium state of the Apennine orogen, in response to changes in wedge dynamics, but also in erosional rates.

2. Calculating exhumation rates from thermochronometric data

The terms "uplift" and "exhumation" have been used rather indiscriminately in the past literature. England

^{*}Corresponding author.

and Molnar (1990) pointed to the importance of a clear distinction for a more rigorous treatment of these processes. They defined "surface uplift" as the displacement of Earth's surface with respect to the geoid; "exhumation" as the displacement of rocks with respect to the surface. The sum of the rates of the first two processes gives the rate of "rock uplift" that is the displacement of rocks with respect to the geoid.

Thermal histories constrained through radiometric systems allowed the exhumation rate to be estimated, but only when certain assumptions are valid, such as the negligible effect of relevant topographic differences (Stüwe et al., 1994) and steady-state isotherms during exhumation (Mancktelow and Grasemann, 1997). In our study areas the first effect can be neglected because of the small wavelength of topography. The second effect has been considered by Brandon et al. (1998), who demonstrated that advection of the isotherms only becomes significant when exhumation rates exceed 1 mm/yr. In these cases, apparent exhumation rates obtained with thermochronological methods can overestimate the real rates.

Two different methods can be used to calculate exhumation rates from mineral cooling ages: (1) the mineral pair method, which uses one rock sample with two (or more) different mineral cooling ages; and (2) the altitude-dependence method, in which analyses are performed on two (or more) samples from different altitudes using the same dating method. In method (1), the assumption of a given value for the geothermal gradient is necessary. This assumption is not required for method (2), but no important tectonic displacement along the vertical profile should have occurred during or after exhumation. If the age of faulting is younger than the youngest isotopic age, then the entire layer of crust now exposed along the vertical profile must have already cooled below the closure temperature ("isotopically closed layer"; Batt, 2001) before the tectonic activity resulting in disruption of the linear relationship between altitude and age. In this work, both the methods have been used with four different chronometers: ZFT, ZHe, AFT and AHe. For our analysis of cooling ages, we use the closure temperature data from Brandon et al. (1998) for AFT and ZFT, Farley (2000) for AHe and Reiners et al. (2002) for ZHe. In order to simplify the analysis, we use a geothermal gradient based on a pre-erosional gradient of 25°C/km (Pasquale et al., 1997) and 10°C of surface temperature. We then iterate to find a best fit average erosion rate from all of our data, which results to be 0.7 mm/yr. Calculation is outlined in Brandon et al. (1998) and accounts for the advection of isotherms due to erosion and the influence of cooling rate on closure temperature. The resulting closure temperatures are 77°C for AHe, 115°C for AFT, 196°C for ZHe and 241°C for ZFT.

2.1. Apuane Alps

The Apuane Alps and Mt. Pisani (Fig. 1) form a ridge parallel to the Tyrrhenian Sea. In this area, the lowermost tectonic units of the Northern Apennines nappe pile are exposed (the metamorphic Tuscan succession and its Paleozoic basement). In the preexhumation configuration, these metamorphic units were overlain by non-metamorphic Mesozoic to Tertiary Tuscan successions and by the Ligurian unit, the uppermost tectonic unit of the Northern Apennines (Carmignani and Kligfield, 1990). Here only the mineral-pair method has been applied. AHe data are not available, but the thermal history has been extended to higher temperatures using ZHe and ZFT data (Table 1). A mean exhumation path has been calculated for two samples of the crystalline basement and one for a sample from the Pseudomacigno (top of the Tuscan metamorphic unit) (Fig. 2). All the three samples show the same ZFT age of about 11 Ma, suggesting that juxtaposition between the basement and its cover had already occurred by this time. Subsequently, all three samples shared a similar cooling path. Between about 11 Ma and about 6 Ma, the cooling rate was between 10°C/Myr and 16°C/Myr which correspond to exhumation rates of 0.4–0.6 mm/yr. Between 6 and 4 Ma, cooling rates increased to between 38°C/Myr and 55°C/Myr equivalent to an exhumation rate of 1.3-1.8 mm/yr. Such an increase of the geothermal gradient from the Messinian onwards is consistent with the onset of the Tuscan geothermal anomaly. The last part of the thermal path is not well constrained due to lack of AHe data, but the average exhumation rate is between 0.6 and 0.9 mm/yr.

2.2. Mt. Falterona

Mt. Falterona, consisting of Miocene foredeep deposits, is located along the present drainage divide (Fig. 1). The reconstructed pre-exhumation configuration shows a thick cover of overlying Ligurian unit which was eroded in the last 5 Myr (Zattin et al., 2000).

Five samples have been collected from the top of Mt. Falterona and along its western flank and dated with AFT (Zattin et al., in press) and AHe methods (Table 2). Assuming a geothermal gradient of 20°C/km (Pasquale et al., 1997), a mean exhumation rate of 0.9 mm/yr was calculated from the differences between the AFT and AHe ages obtained from the same samples (AP45, mineral-pair method; Fig. 3).

In an altitude–age diagram (Fig. 4), the regression line for the AFT ages has a poor fit, because of the large analytical error and the effects of post-cooling tectonics that likely disrupted the vertical profile. The regression line between AHe ages gives a reliable value of exhumation rate of 0.7 mm/yr (line A in Fig. 4).



Fig. 1. Schematic geologic map of Northern Apennines. AP: Apuane Alps; MF: Mt. Falterona; MP: Monti Pisani; Sa: Sarzana basin; AO: Aulla-Olivola basin; S: Serchio basin; M: Mugello basin; C: Casentino basin.

Table 1 ZFT data												
Sample	Elevation (m)	No. of grains	$ ho_{\rm d}$	N _d	$ ho_{\rm s}$	$N_{\rm s}$	$ ho_{ m i}$	N_{i}	Age (Ma)	-2SE	+2SE	$P(\chi^2)$ (%)
G3 CIP3 AR2	170 650 840	10 10 10	$\begin{array}{c} 2.858\mathrm{E} + 05\\ 2.825\mathrm{E} + 05\\ 2.813\mathrm{E} + 05\end{array}$	3180 3143 3130	1.72E + 06 1.38E + 06 2.25E + 06	171 132 212	8.14E + 06 6.04E + 06 9.95E + 06	809 577 937	10.1 10.8 10.6	1.6 1.9 1.5	1.8 2.3 1.7	98.9 67.5 14.8

Note: All samples were dated with the external detector method for fission-track dating by M. Bernet. Zircon grains were mounted in $2 \times 2 \text{ cm}^2$ squares of FEP TeflonTM. During polishing, each mount was first cut with 800 grit wet sandpaper, and then polished successively on 9 and 1 µm diamond paste. All mounts were etched in a eutectic NaOH–KOH mixture at exactly 228°C. After etching, mounts were covered with a low-uranium mica detector, and irradiated with thermal neutrons at Oregon State University with a normal fluence of $2 \times 10^{15} \text{ n/cm}^2$, along with zircon age standards (Buluk Tuff and Fish Canyon Tuff) and a reference glass dosimeter CN-5. Samples were counted at $1250 \times \text{dry} (100 \times \text{objective}, 1.25 \text{ tube} factor, 10 \text{ oculars})$ using a zeta (CN-5) of $334.22 \pm 3.40 (\pm 1 \text{ SE}; \text{MB})$. ρ_d is the effective track density for the fluence monitor (tracks/cm²) and N_d is the number of tracks in the fluence monitor. ρ_s is the spontaneous track density in the grain and N_s the number of spontaneous tracks (tracks/cm²). $P(C_2)$ is the probability of obtaining C_2 value (Galbraith, 1981)

Although the value is coherent with the rate calculated with the mineral-pair method, the effects of postexhumation tectonics must be considered. An important extensional fault, interrupting the AHe cooling trend exists between the two lowermost samples. This fault was active in the last two million years, as part of the normal fault system responsible of formation of the Pleistocene intramontane basins. Therefore, a more reliable AHe regression line can be determined excluding the lowermost sample giving a revised rate of exhumation of 0.6 mm/yr (line B in Fig. 4). In fact, the postcooling displacement of this extensional fault can be calculated from projection of the lowermost sample onto the regression line (see Fig. 4), implying an offset of ca. 540 m.

3. Combining thermochronometric and regional geological data

In order to investigate the relationships between exhumation, surface uplift and rock uplift, exhumation rates derived from thermochronological data can be integrated with information on the evolution of the topographic relief. Sedimentation in adjacent continental basins is a discontinuous archive of the topographic evolution of the adjacent ridges. In the basins bordering the Apuane (Sarzana, Aulla-Olivola, Serchio) and Falterona ridges (Casentino-Mugello) (see Fig. 1), the stratigraphy shows an initial discontinuous coarsegrained unit, followed by a more widespread and thicker fine-grained lacustrine unit, possibly bordered by fan deltas (Cavinato and De Celles, 1999). The uppermost unit consists of unconformable coarse-grained alluvial deposits (Calistri, 1974; Benvenuti, 1997). We interpret this succession as the record of the inception, growth and final infilling of the basins. Such an evolution corresponds to the onset of surface uplift, dated by the first deposits (minimum age), and continuous growth of



Fig. 2. Exhumation path for the Apuane Alps (mineral-pair method). Bars indicate $\pm 1\sigma$ errors for ages. Squares: crystalline basement; triangles: Pseudomacigno.

Table 2			
U-Th/He zircon	and	apatite	data

the adjacent ridges. However, we envisage a prevalent role of climate in controlling the timing of the abrupt facies changes. Most of the fine-grained lacustrine deposits occur in the Early Pliocene (Aulla-Olivola) and Early Pleistocene (Mugello), periods characterized by equable humid climate and low seasonality (Suc, 1984; Pasini and Colalongo, 1997). The transition to the overlying coarse-grained alluvial deposits is sharp and erosive. It likely documents an abrupt climatic change towards a cooler climate, characterized by enhanced variability, strong seasonality and even glaciations, as documented for the Middle-Late Pliocene and the Middle-Late Pleistocene by Suc (1984). As a conclusion, the deposition of the topmost alluvial unit documents an already existing topography, whereas the timing of its deposition is controlled by a climatic transition conducive to mechanical erosion.



Fig. 3. Exhumation path for the Mt. Falterona sample AP45 (mineralpair method). The temperatures have been converted into elevation assuming a geothermal gradient of 20° C/km. Bars indicate $\pm 1\sigma$ errors for ages.

U-In/ite zhoon and apatite data								
Sample	Elevation (m)	mineral	FT*	$Age \pm 2\sigma$ (Ma)	U (ppm)	Th (ppm)		
Apuane Alps								
AR2A	840	Zircon	0.75	7.42 ± 0.59	619.8	249.4		
CIP3A	650	Zircon	0.70	4.98 ± 0.40	165.0	57.1		
G3A	170	Zircon	0.83	5.70 ± 0.46	91.9	36.8		
Mt. Falterona								
Ap43A	515	Apatite	0.61	2.72 ± 0.16	31.6	61.2		
Ap44A	725	Apatite	0.80	2.45 ± 0.15	29.3	54.6		
Ap45A	940	Apatite	0.70	2.59 ± 0.16	32.7	67.5		
Ap47A	1365	Apatite	0.76	2.81 ± 0.17	28.8	50.5		
Ap48A	1655	Apatite	0.74	3.81 ± 0.23	30.7	41.5		

Note: All samples were analyzed by P. Reiners. FT* is fraction of alphas retained; U, Th: Uranium and Thorium contents.

3.1. Apuane Alps

We have no geological constraints regarding the relief in the Apuane Alps in the 11-6 Ma interval. If no surface uplift is presumed, then the total rock uplift rate must equal the exhumation rate (0.4–0.6 mm/yr). The first record of the existence of relief is documented by



Fig. 4. Exhumation path for the Mt. Falterona (altitude-dependence method). Bars indicate $\pm 1\sigma$ errors for ages. Line A has been calculated considering all the samples, whereas the lowermost sample was not considered for line B.

Early Pliocene (Ruscinian) lacustrine sediments in the Aulla-Olivola basin, northwest of the Apuane Alps (Bertoldi, 1988). At the end of Early Pliocene (Early Villafranchian), a lake developed in the tectonic depression of the Serchio basin, east of the Apuane Alps (Calistri, 1974). Our data indicate that the rock uplift rate must have been at least 1.3-1.8 mm/yr (i.e. \geq exhumation rate) to allow for surface uplift between 6 and 4 Ma. It may be possible that this estimate is higher than the real rate due to advection of isotherms and possible variations in the closure temperatures. Nevertheless, the increase in exhumation rates is undeniable. Between ca. 4 Ma to present, thermochronological data document a decrease in the exhumation and hence in rock uplift rate, although a better evaluation is prevented by lack of AHe data.

3.2. Mt. Falterona

Geological data suggest that little or no topography was present between 5 and 2 Ma (Benvenuti, 1997). Therefore, rates of rock uplift and exhumation must have been nearly equivalent (0.7–0.9 mm/yr, Figs. 3 and 4). Graben deposits in the Casentino and Mugello basins indicate that some relief was present since at least 1.5 Ma (Benvenuti, 1997). The present topographic relief results from an increase in the rock uplift rates to at least 1.7 mm/yr (Fig. 3).



Fig. 5. Exhumation history of the two key areas from the Late Miocene onward. Arrow length is proportional to the uplift rate.

4. Exhumation processes: the roles of erosion and tectonics

Between 11 and 6 Ma, the Apuane Alps were exhumed at a constant rate of about 0.4–0.6 mm/yr, whilst the Mt. Falterona area was rapidly subsiding, buried by foreland turbidites and eventually by the Ligurian unit. Exhumation rates in the Apuane Alps increased in the Messinian to 1.3–1.8 mm/yr. After the Early Pliocene, exhumation rates dropped to about 0.7 mm/yr. At this time, the Mt. Falterona started to be exhumed at a similar rate of 0.7–0.9 mm/yr. From Early Pleistocene onward, the rock uplift rates increased to values of more than 1.7 mm/yr, leading to the present day topography (Fig. 5).

The data indicate that the long-term exhumation of the chain occurred at an average rate, estimated to be about 0.7 mm/yr since at least 11 Ma. This value is not far from the estimated erosion rates for Quaternary times calculated from the sediment volume deposited in the Northern Apennines Quaternary foredeep (0.4–0.5 mm/yr, Bartolini et al., 1996). Interestingly, a similar value (0.6 mm/yr) was estimated by Hinderer (2001) for the Quaternary erosion of the Alpine chain. However, periods of increased exhumation up to 1.7-1.8 mm/yr have been calculated both in the Apuane Alps and in the Mt. Falterona area. Since these periods are almost coeval with the appearance of intramontane deposits in the adjacent basins, we envisage that surface uplift must also have initiated at those times to allow the creation of topographic relief. It can be argued that the estimated exhumation rate of about 0.7 mm/yr could be considered as a threshold value: higher exhumation/ erosion rates indicate a growing relief produced by an increase in rock uplift rate (possibly tectonically induced); at lower rates, erosion balances the rock uplift and the mean topographic surface approaches a steady elevation. Climate and above all, lithology are undoubtedly primary factors in controlling the threshold exhumation value and any estimate of it should not be generalized.

Thermochronological data show that the acceleration of the exhumation rates in the Mt. Falterona area took place about 3 Myr later than the onset of similar exhumation in the Apuane Alps. The same time gap is also reflected by extensional tectonic activity, which started on Tyrrhenian side and then moved towards the east. Therefore, we propose that local tectonics (in the form of normal faulting) contributed to the formation of relief, whereas erosional exhumation driven by deeper processes dominates over the long-term period.

Acknowledgements

The manuscript was improved by a helpful review by S.N. Thomson and by constructive discussions with

L. Piccini and C. Bartolini. This work was supported in part by MURST ex-40% 1997–1999.

References

- Abbate, E., Balestrieri, M.L., Bigazzi, G., Norelli, P., Quercioli, C., 1994. Fission-track dates and recent rapid denudation in Northern Apennines, Italy. Memorie Società Geologica Italiana 48, 579–585.
- Abbate, E., Balestrieri, M.L., Bigazzi, G., Ventura, B., Zattin, M., Zuffa, G.G., 1999. An extensive apatite fission-track study throughout the Northern Apennines nappe belt. Radiation Measurements 31, 673–676.
- Bartole, R., 1995. The North Tyrrhenian–Northern Apennines postcollisional system: constraints for geodynamic model. Terra Nova 7, 7–30.
- Bartolini, C., 2003. When did the Northern Apennine become a mountain chain? Journal of Quaternary International, this issue.
- Bartolini, C., Caputo, R., Pieri, M., 1996. Pliocene-Quaternary sedimentation in the Northern Apennine Foredeep and related denudation. Geological Magazine 133, 255–273.
- Batt, G.E., 2001. The approach to steady-state thermochronological distribution following orogenic development in the Southern Alps of New Zealand. American Journal of Science 301, 374–384.
- Benvenuti, M., 1997. Physical stratigraphy of the fluvio-lacustrine Mugello Basin (Plio-Pleistocene, northern Apennines, Italy). Giornale di Geologia 59, 91–111.
- Bertoldi, R., 1988. Una sequenza palinologica di età rusciniana nei sedimenti lacustri basali del bacino di Aulla-Olivola (Val Magra). Rivista Italiana di Paleontologia e Stratigrafia 94, 105–138.
- Brandon, M., Roden-Tice, M.K., Garver, J.I., 1998. Late Cenozoic exhumation of the Cascadia accretionary wedge in the Olympic Mountains, NW Washington State. Geological Society of America Bulletin 110, 985–1009.
- Calistri, M., 1974. Il Pliocene fluvio-lacustre della Conca di Barga. Memorie della Società Geologica Italiana 13, 1–21.
- Carmignani, L., Kligfield, R., 1990. Crustal extension in the Northern Apennines: the transition from compression to extension in the Alpi Apuane core complex. Tectonics 9, 1275–1303.
- Cavinato, G.P., De Celles, P., 1999. Extensional basins in the tectonically bimodal central Apennines fold-thrust belt, Italy: response to corner flow above a subducting slab in retrograde motion. Geology 27, 955–958.
- D'Agostino, N., Jackson, J.A., Dramis, F., Funiciello, R., 2001. Interactions between mantle upwelling, drainage evolution and active normal faulting: an example from the central Apennines (Italy). Geophysical Journal International 147, 475–497.
- Elter, P., Giglia, G., Tongiorgi, M., Trevisan, L., 1975. Tensional and compressional areas in the recent (Tortonian to Present) evolution of the Northern Apennines. Bollettino Geofisica Teorica e Applicata 17, 3–18.
- England, P., Molnar, P., 1990. Surface uplift, uplift of rocks, and exhumation of rocks. Geology 18, 1173–1177.
- Farley, K.A., 2000. Helium diffusion from apatite: general behaviour as illustrated by Durango fluoroapatite. Journal of Geophysical Research 105, 2903–2914.
- Galbraith, R.F., 1981. On statistical models of fission track count. Mathematical Geology 13, 471–488.
- Hinderer, M., 2001. Late Quaternary denudation of the Alps, valley and lake fillings and modern river loads. Geodinamica Acta 14, 231–263.
- Leeder, M.R., Jackson, J.A., 1993. The interaction between normal faulting and drainage in active extensional basins, with examples

from the western United States and central Greece. Basin Research 5, 79–102.

- Malinverno, A., Ryan, W.B., 1986. Extension in the Tyrrhenian Sea and shortening in the Apennines as a result of arc migration driven by sinking of the lithosphere. Tectonics 5, 227–246.
- Mancktelow, N.S., Grasemann, B., 1997. Time-dependent effects of heat advection and topography on cooling histories during erosion. Tectonophysics 270, 167–195.
- Martini, I.P., Sagri, M., Colella, A., 2001. Neogene-Quaternary basins of the inner Apennines and Calabrian Arc. In: Vai, G.B., Martini, I.P. (Eds.), Anatomy of an Orogen: the Apennines and Adjacent Mediterranean Basins. Kluwer Academic Publishers, Dordrecht, pp. 375–400.
- Masek, J.G., Isacks, B.L., Fielding, E.J., Browaeys, J., 1994. Rift-flank uplift in Tibet: evidence for crustal asthenosphere. Tectonics 13, 659–667.
- Pasini, G., Colalongo, M.L., 1997. The Pleistocene boundary stratotype at Vrica, Italy. In: Van Couvering, J.A. (Ed.), The Pleistocene Boundary and the Beginning of the Quaternary. Cambridge University Press, Cambridge, pp. 15–45.

- Pasquale, V., Verdoya, M., Chiozzi, P., Ranalli, G., 1997. Rheology and seismotectonic regime in the northern central Mediterranean. Tectonophysics 270, 239–257.
- Reiners, P.W., Farley, K.A., Hickes, H.J., 2002. He diffusion and (U–Th)/He thermochronometry of zircon: initial results from Fish Canyon Tuff and Gold Butte, Nevada, Tectonophysics 349, 297–308.
- Royden, L.H., 1993. Evolution of retreating subduction boundaries formed during continental collision. Tectonics 12, 629–638.
- Stüwe, K., White, L., Brown, R., 1994. The influence of eroding topography on steady-state isotherms. Application to fission-track analysis. Earth and Planetary Sciences Letters 124, 63–74.
- Suc, J.P., 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. Nature 307, 429–432.
- Zattin, M., Landuzzi, A., Picotti, V., Zuffa, G.G., 2000. Discriminating between tectonic and sedimentary burial in a foredeep succession, Northern Apennines. Journal of the Geological Society of London 157, 629–633.
- Zattin, M., Picotti, V., Zuffa, G.G. Fission-track reconstruction of the front of the Northern Apennine thrust wedge and overlying Ligurian unit. American Journal of Science, in press.