J. Math. Kyoto Univ. (JMKYAZ)
25-4 (1985) 775-788

Existence and uniqueness of solutions for a diffusion model of intergroup selection

Dedicated to Professor Sigeru Mizohata on his sixtieth birthday

By

Norio SHIMAKURA

(Received October 8, 1984)

In this memoir, we consider an initial boundary value problem proposed by M. Kimura [1] as a diffusion model of intergroup selection in population genetics. The purpose of the present paper is to prove the existence of solutions and, under a stronger assumption, the uniqueness of the solution.

The unknown function $U=U(t, x)$ is the distribution function of a random variable x running over the interval $[0, 1]$. x is the frequency of an allele of "altruistic" character and t is the time variable representing the generation. The main equation for U is a partial differential equation of parabolic type degenerated at $x=0$ and $x=1$. This equation is non-linear but the non-linearity is not so strong that we can treat it as a linear one.

To prove the uniqueness of the solutions, we show the continuity of the dependence of solutions on the initial values, not with respect to the strong topology in L^1-space but with respect to the topology in the space of the moment sequences of solutions. In the proof of existence, we discuss the approximative solutions also in the latter sense of convergence. Therefore, the use of moment sequences is essential in our reasoning. The main theorem of the present paper will be stated in §3.

§1. The initial boundary value problem

In this §1, let us formulate an initial boundary value problem proposed by M. Kimura [1], which we call the problem (P).

Let N, v, v', s and m be given real numbers. We assume that N be a positive integer, s and m be positive, v and v' be non-negative. Let us give also a real-valued continuous function $c(x)$ on the interval $[0, 1]$.

We shall find a function $U(t, x)$ defined on the interval $[0, +\infty)\times(0, 1)$ satisfying, at first,

(P.1) $\quad U(t, x)\geq 0$ in $[0, +\infty)\times(0, 1)$ and $\int_0^1 U(t, x)dx<+\infty$;

a partial differential equation of parabolic type

$$\frac{\partial U}{\partial t}(t, x)=\frac{\partial^2}{\partial x^2}\left\{\frac{x(1-x)}{4N}U(t, x)\right\}-\frac{\partial}{\partial x}[\{v'(1-x)-vx-$$

(P.2) $$-sx(1-x)+m(\bar{x}(t)-x)\}U(t, x)]+\{c(x)-\bar{c}(t)\}U(t, x),$$

$$\text{in} \quad (0, +\infty)\times(0, 1);$$

with

(P.3) $$\bar{x}(t)=\int_0^1 xU(t, x)dx/\int_0^1 U(t, x)dx,$$

$$\bar{c}(t)=\int_0^1 c(x)U(t, x)dx/\int_0^1 U(t, x)dx;$$

the zero-flux boundary condition

(P.4) $$\frac{\partial}{\partial x}\left\{\frac{x(1-x)}{4N}U(t, x)\right\}-\{v'(1-x)-vx-sx(1-x)+m(\bar{x}(t)-x)\}U(t, x)$$

tends to zero as $x\searrow 0$ or as $x\nearrow 1$;

and the initial condition

(P.5) $$U(0, x)=\lim_{t\searrow 0} U(t, x)=\phi(x) \quad \text{in} \quad (0, 1),$$

where the function $\phi(x)$ is assumed to satisfy

(P.6) $$\phi(x)\geq 0 \quad \text{in} \quad (0, 1) \quad \text{and} \quad \int_0^1 \phi(x)dx=1.$$

We shall call the problem (P) the set of constraints (P.1), (P.2), (P.3), (P.4), (P.5) and (P.6).

Let U be a solution of (P). Integrating the both sides of (P.2) taking account of (P.3) and (P.4), we have

$$\frac{d}{dt}\int_0^1 U(t, x)dx=0.$$

The initial value being normalized as in (P.6), we have

(7) $$\int_0^1 U(t, x)dx=1 \quad \text{at any} \quad t\geq 0.$$

So, the quantities $\bar{x}(t)$ and $\bar{c}(t)$ can be expressed as

(P.3′) $$\bar{x}(t)=\int_0^1 xU(t, x)dx \quad \text{and} \quad \bar{c}(t)=\int_0^1 c(x)U(t, x)dx$$

abbreviating the denominators.

In the analysis of the present paper, the assumptions above on s, m, v and v' will be essentially used to obtain non-negative solutions U. But the assumption that

N be a positive integer is of no importance. It suffices for N to be positive. On the other hand, the continuity assumption on $c(x)$ makes the problem easy to solve. The author expects that the proof of the existence theorem stated in §3 remains true without any change if $c(x)$ is bounded and Borel measurable.

§2. Background of the problem in population genetics

Following M. Kimura [1], let us explain briefly the meaning of our problem in population genetics.

Let us consider a hypothetical population (species) consisting of an infinite number of competing subgroups (demes). Each of demes is assumed to have an equal effective size N independently of time (generation) t.

Let us consider a pair of alleles A and A' at a particular gene locus, where we refer to A' as "altruistic allele". We denote by $x(0 \leq x \leq 1)$ the frequency of A' in a deme and consider the frequency distribution of x among the enitre collection of demes making up the species. Let $U(t, x)$ be the distribution function of x at time t such that $U(t, x)\Delta x$ represents the fraction of demes whose frequency of A' is in the interval $(x, x+\Delta x)$.

In each generation, mutation occurs from A to A' at the rate of v' (≥ 0) and from A' to A at the rate of $v\,(\geq 0)$. So, the rate of change in x by mutation is $v'(1-x)-vx$.

A' is assumed to have selective disadvantage s (>0) relative to A. So, the rate of change in x by individual selection is $-sx(1-x)$.

Migration is assumed to occur in the following way: each deme contributes emigrants to the entire gene pool of the species at the rate m (>0) and receives immigrants from that pool at the same rate. So, if $\bar{x}(t)$ is the average frequency of A' in the entire species, the rate of change in x in a given deme by migration is $m(\bar{x}(t)-x)$.

Moreover, let us assume the effect of interdeme selection. We denote by $c(x)$ the coefficient of interdeme selection. This represents the rate at which the number of demes belonging to the gene frequency class x changes through interdeme competition. That is, during a short time interval $(t, t+\Delta t)$, the change of U is

$$\Delta U = \frac{1+c(x)\Delta t}{1+\bar{c}(t)\Delta t}\,U - U \fallingdotseq \{c(x)-\bar{c}(t)\}U\Delta t,$$

where $\bar{c}(t)$ is the average of $c(x)$ over the entire array of demes in the species.

Taking account all of mutation, individual selection, migration and interdeme competition, we have the main equations (P.2) and (P.3) in §1. The zero flux condition (P.4) says that the total mass of U in the interval (0, 1) is always equal to 1 and that the paths of the stochastic process are almost surely continuous.

The "altruistic" character of A' means that the disadvantage in individual selection is recovered by the advantage in interdeme competition. Therefore, it may be natural to assume that $c(x)$ be an increasing function of x. M. Kimura [1] considers the case where $c(x)=cx$ with a positive constant c. Mainly by a numerical analysis of steady state solutions, Kimura finds that $\bar{x}$ (the mean of x) is nearly equal to 1 if $D>0$ and to 0 if $D<0$, where $D=(c/m)-4Ns$. And he concludes as follows: If $D>0$, the intergroup competition prevails over the individual selection and the altruistic allele A' predominates. If, on the contrary, $D<0$, A' becomes rare and cannot be established in the species.

In this paper, no qualitative assumption is made for $c(x)$ other than smoothness assumptions.

§ 3. Statement of results

Theorem. (i) *If $c(x)$ is real-valued continuous function defined on* $[0, 1]$, *the initial boundary value problem* (*P*) *has a solution $U(t, x)$ for any given initial value $\phi(x)$ satisfying* (*P*.6).

(ii) *If, moreover, $c(x)$ is real analytic and if it has Taylor expansion*

$$c(x)=\sum_{n=0}^{\infty} c_n\left(x-\frac{1}{2}\right)^n \qquad \textit{with} \quad \overline{\lim_{n\to\infty}}\, |c_n|^{1/n}<2,$$

then the solution is unique.

Remark. It is quite natural to expect that $U(t, x)$ may be positive in the region $(0, \infty)\times(0, 1)$. If we assume that $c(x)$ be real analytic in $(0, 1)$, we can prove it very easily as follows.

Since U is assumed to be non-negative, it suffices to show that U does never vanish. Suppose, on the contrary, that $U(t^\circ, x^\circ)=0$ at some point $(t^\circ, x^\circ)\in(0, \infty)\times(0, 1)$. Note that U is of class C^∞ in (t, x) and real analytic in x when $t>0$. Let us expand $U(t^\circ, x)$ in Taylor series at $x=x^\circ$:

$$U(t^\circ, x)=\sum_{p=0}^{\infty}\frac{(x-x^\circ)^p}{p!}\frac{\partial^p U}{\partial x^p}(t^\circ, x^\circ).$$

We can show, by induction on n, that

$$\frac{\partial^{p+q}U}{\partial t^p\partial x^q}(t^\circ, x^\circ)=0 \quad \text{if} \quad 2p+q=n \quad \text{for} \quad n=0, 1, 2,\dots$$

Hence, the Taylor series is zero, so $U(t^\circ, x)$ is identically zero. This is absurd because the total mass of U is equal to 1 at any time. Consequently, U is positive in the region $(0, \infty)\times(0, 1)$.

It is very interesting to study the behavior of $\bar{x}(t)$ as a function of t. Assuming here a differential equation (see (2) of §4)

$$\text{(1)} \qquad \frac{d\bar{x}}{dt}+(v+v'+s)\bar{x}-v'-sM_2 = \int_0^1\int_0^1 \{c(x)-c(y)\}xU(t, x)U(t, y)dxdy,$$

we can show a very rough estimate for $\bar{x}(t)$:

Proposition. *Let us put* $C = \mathrm{Max}\,\{|c(x)-c(y)|;\ 0 \leq x,\ y \leq 1\}$. *Then,* $\bar{x}(t)e^{(v+v'+s+C)t}$ *and* $(1-\bar{x}(t))e^{(v'+C)t}$ *are inceasing functions of t. If, in particular,* $c(x)$ *is non-decreasing,* $\bar{x}(t)e^{(v+v'+s)t}$ *is increasing.*

Proof. We can replace the factor x in the integral of the right hand side also by $x-1$. So, the absolute value of this integral is less than $\mathrm{Max}\,\{C\bar{x},\ C(1-\bar{x})\}$. In addition, $\bar{x}^2 < M_2 < \bar{x}$. We have therefore

(2) $$s\bar{x}^2-(v+v'+s+C)\bar{x}+v' < \frac{d\bar{x}}{dt} < (v'+C)(1-\bar{x})-v\bar{x}.$$

Let us neglect the terms $s\bar{x}^2+v'$ on the left hand side and $-v\bar{x}$ on the right hand side. Then, we have the first assertions of lemma. Next, we assume that $c(x)$ be non-decreasing. In the integral of the right hand side of (1), we replace the factor x by $(x-y)/2$. Then we see that the integral is non-negative. So, we can neglect the terms $s\bar{x}^2 - C\bar{x}+v'$ on the left hand side of (2). Thus, the last assertion of lemma is also correct.

Suppose now that v and v' be positive. Let us denote by $\underline{a}$ the root in the interval (0, 1) of the equation $s\underline{a}^2-(v+v'+s+C)\underline{a}+v'=0$. Put also $\bar{a}=(v'+C)/(v+v'+C)$ (so $0<\underline{a}<\bar{a}<1$). Moreover, let us define an interval I as follows: $I=[\bar{x}(0),\ \bar{a})$ if $0<\bar{x}(0)\leq\underline{a}$, $I=(\underline{a},\ \bar{a})$ if $\underline{a}<\bar{x}(0)<\bar{a}$ and $I=(\underline{a},\ \bar{x}(0)]$ if $\bar{a}\leq\bar{x}(0)<1$. Then we have

Corollary. *If* $v>0$ *and* $v'>0$, $\bar{x}(t)$ *lies in the interval I defined above at any* $t \geq 0$.

Proof. The left hand side of (2) is positive if $0<\bar{x}<\underline{a}$ and zero if $\bar{x}=\underline{a}$, while the right hand side is negative if $\bar{a}<\bar{x}<1$ and zero if $\bar{x}=\bar{a}$. So the assertion follows from (2).

Therefore, if $U(x)$ is a steady state solution of (P) (that is, a solution inedpendent of t), the mean value $\bar{x}$ of x is in the interval $(\underline{a},\ \bar{a})$.

§4. An alternative formulation of the problem

Let $U(dx)$ be a Stieltjes measure on [0,1]. Since the polynomials are dense in the Banach space of all continuous functions on [0, 1], $U(dx)$ is characterized by its moment sequence $\{M_k\}_{k=0}^{\infty}$ which is by definition

$$M_k = \int_0^1 x^k U(dx) \qquad \text{for} \quad k=0,\ 1,\ 2,\dots .$$

If $U(dx)$ is a probability measure, this sequence satisfies the following conditions

(a) $$M_0=1; \quad \text{(b)} \quad \sum_{p=0}^{n}(-1)^p\binom{n}{p}M_{k+p}\geq 0 \quad \text{for all} \quad k,\ n=0,\ 1,\ 2,\dots$$

Conversely, any sequence $\{M_k\}_{k=0}^{\infty}$ satisfying (a) and (b) is the moment sequence of a probability Stieltjes measure (see Chap. III of D. Widder [2] for this context).

Therefore, to obtain a solution $U(t, x)$ of our problem (P), it suffices to determine its moment sequence. Let $U(t, x)$ be a solution of (P). Writing $U(t, dx)$ instead of $U(t, x)dx$, let us put

$$M_k(t)=\int_0^1 x^k U(t, dx) \quad \text{for} \quad t\geq 0 \quad \text{and} \quad k=0, 1, 2,... \tag{1}$$

Multiplying x^k to the both sides of (P.2) and integrating over (0, 1), we have the following system of differential equations, where the vanishing of all the boundary terms appearing by integration by parts is assumed here and will be proved by the next lemma.

$$\begin{aligned} &\frac{d}{dt} M_k(t)+k\left(v+v'+s+m+\frac{k-1}{4N}\right)M_k(t)= \\ &=ksM_{k+1}(t)+k\left(v'+mM_1(t)+\frac{k-1}{4N}\right)M_{k-1}(t)+ \\ &+\int_0^1\int_0^1 \{c(x)-c(y)\}x^k U(t, dx)U(t, dy), \quad \text{if} \quad t>0. \end{aligned} \tag{2}$$

And the initial condition for $\{M_k(t)\}$ is given

$$M_k(0)=\int_0^1 x^k\phi(x)dx \quad \text{for} \quad k=0, 1, 2,... \tag{3}$$

Lemma . (i) *If $U(t, x)$ is a solution of the problem (P), its moment sequence $\{M_k(t)\}_{k=0}^{\infty}$ satisfies (a), (b), (2) and (3) above.*
(ii) *Conversely, let $\{U(t, dx); t\geq 0\}$ be a family of Stieltjes measures on [0, 1] whose moment sequences satisfy (a), (b), (2) and (3). Then, at any $t\geq 0$, $U(t, dx)$ has a density $U(t, x)$ which is a solution of (P).*

Proof. Let U be a solution of (P). Let us show that

$$x(1-x)U(t, x)\to 0 \quad \text{as} \quad x\searrow 0 \quad \text{or as} \quad x\nearrow 1, \quad \text{if} \quad t>0. \tag{4}$$

The boundary condition (P.4) implies that $\frac{d}{dx}\{x(1-x)U\}$ is integrable, so that $x(1-x)U$ has finite limits as $x\searrow 0$ or as $x\nearrow 1$. If one of these limits were not zero, U is no more integrable near that end point. Hence, (4) is true and the calculus to obtain (2) is justified. Thus, (i) is proved.

To prove (ii), let us verify the following identity for any function $f(t, x)$ of class C^1 in t on $[0, \infty)$ and of class C^2 in x on [0, 1]:

$$\begin{aligned} \frac{d}{dt}\int_0^1 f(t, x)U(t, dx)=\int_0^1\Big[&\frac{\partial f}{\partial t}+\frac{x(1-x)}{4N}\frac{\partial^2 f}{\partial x^2}+\{v'(1-x)-vx \\ &-sx(1-x)+m(\bar{x}(t)-x)\}\frac{\partial f}{\partial x}+\{c(x)-\bar{c}(t)\}f\Big]U(t, dx). \end{aligned} \tag{5}$$

By (2) and a simple computation, (5) is verified for polynomials f in t and x, so it is true for any f with regularity as above. Hence, $U(t, dx)$ is a solution of (P.2) in the sense of distribution. $U(t, dx)$ has a density $U(t, x)$ (satisfying (P.4) and (4) above) with the following smoothness in the region $(0, \infty)\times(0, 1)$: for any $\delta(0<\delta<1)$, U is Hölder continuous of exponent $(1+\delta)/2$ in t, $\partial U/\partial x$ is Hölder continuous of exponent $\delta/2$ in t and of exponent δ in x. To see this, we use the fundamental solution of the equation $V_t=V_{yy}(\bar{x}(t)$ is of class C^1 and $\bar{c}(t)$ is continuous. So, by a change of variables $(t, x)\to(t, y(x))$ and $U(t, x)=a(t, y)V(t, y)$, (P.2) is locally reduced to an equation of type $V_t=V_{yy}+b(t, y)V$, where b is a continuous function). (5) implies (P.4) and (4), (P.5) is nothing but (3) and (P.1) holds because of (b). (ii) is proved.

To determine $\{M_k(t)\}_{k=0}^{\infty}$, the system (a)–(b)–(2)–(3) is not closed in itself because (3) contains $U(t, dx)$ on the right hand side. But, if we assume the Taylor expansion

(6) $$c(x)=\sum_{n=0}^{\infty}\gamma_n x^n \qquad \text{with} \quad \overline{\lim_{n\to\infty}}|\gamma_n|^{1/n}<1,$$

this integral can also be expressed by means of $\{M_k(t)\}$:

(7) $$\begin{aligned}&\int_0^1\int_0^1\{c(x)-c(y)\}x^k U(t, dx)U(t, dy)=\\ &\quad=\sum_{n=0}^{\infty}\gamma_n\{M_{k+n}(t)-M_k(t)M_n(t)\}.\end{aligned}$$

In this case, our initial boundary value problem (P) is explicitly reformulated as a problem to find a family of moment sequences $\{\{M_k(t)\}_{k=0}^{\infty}\,;\, t\geq 0\}$ satisfying (a)–(b)–(2)–(3) above. The author was inspired by a formula in M. Kimura [1] analogous to (5) above.

§5. Uniqueness of the solution

To prove the uniqueness of the solution of (P), it suffices to show the uniqueness of the moment sequence of the solution. However, under the hypothesis in (ii) of the theorem, the following sequence $\{L_k(t)\}_{k=0}^{\infty}$ is more convenient to treat than the moment sequence itself:

(1) $$L_k(t)=\int_0^1\left(x-\frac{1}{2}\right)^k U(t, x)dx \qquad \text{for} \quad k=0, 1, 2,\ldots$$

For each k, M_k is a linear combination of $L_0,\ldots, L_k$ and vice versa. So, our task is to show the uniqueness of $\{L_k(t)\}$.

Let U and $\tilde{U}$ be two solutions of (P), where the initial values of U and $\tilde{U}$ may be different but they are assumed to satisfy (P.6). Let $\{L_k(t)\}$ and $\{\tilde{L}_k(t)\}$ be the sequences defined by (1) for U and $\tilde{U}$ respectively. Let us consider the following quantity to estimate $\tilde{U}-U$:

(2) $$E(t)=\sum_{k=0}^{\infty}R^k\{\tilde{L}_k(t)-L_k(t)\}^2=E(t;\, \tilde{U}-U),$$

$$\text{where} \quad \rho^2<R<4 \qquad \text{with} \quad \rho=\overline{\lim_{n\to\infty}}|c_n|^{1/n} \quad (<2).$$

The series is absolutely convergent because $|L_k(t)| \leq 2^{-k}$ and $|\tilde{L}_k(t)| \leq 2^{-k}$ by definition.

The following lemma shows that any solution depends continuously on the initial value. If we apply it to U and $\tilde{U}$ with the same initial value, we have at once $E(t) \equiv 0$ so that $\tilde{U}(t, x) \equiv U(t, x)$. Therefore, the uniqueness of the solution is established.

Lemma. Under the assumption in (ii) of the theorem, we have

$$E(t) \leq E(0)e^{Bt} \quad \text{for all} \quad t \geq 0, \tag{3}$$

where B is a real constant independent of U and $\tilde{U}$ (depending only on N, v, v', s, m, $c(x)$ and R).

Proof. We can differentiate $E(t)$ term by term with respect to t, because, as we shall see below, $|dL_k/dt| \leq A'k^2 2^{-k}$ with some constant A' independent of k (the same is true for $d\tilde{L}_k/dt$). We are going to show that

$$\frac{d}{dt} E(t) \leq BE(t). \tag{4}$$

Quite similarly as (2) of §4, we can write down the differential equations for $\{L_k\}$ and for $\{\tilde{L}_k\}$:

$$\frac{d}{dt} L_k + k\left(v + v' + m + \frac{k-1}{4N}\right) L_k = ksL_{k+1} + k\left(\frac{v'-v}{2} - \frac{s}{4} + mL_1\right) L_{k-1}$$
$$+ \frac{k(k-1)}{16N} L_{k-2} + \sum_{n=1}^{\infty} c_n (L_{k+n} - L_k L_n)$$

Let us put $D_k = \tilde{L}_k - L_k$. Then, they satisfy

$$\begin{aligned} &\frac{d}{dt} D_k + k\left(v + v' + m + \frac{k-1}{4N}\right) D_k = ksD_{k+1} + k\left(\frac{v'-v}{2} - \frac{s}{4} + m\tilde{L}_1\right) D_{k-1} \\ &+ \frac{k(k-1)}{16N} D_{k-2} + kmL_{k-1}D_1 + \sum_{n=1}^{\infty} c_n (D_{k+n} - \tilde{L}_k D_n - L_n D_k). \end{aligned} \tag{5}$$

On the other hand, take an r such that $\rho < r < \sqrt{R}$. Then, by hypothesis on $c(x)$, we have

$$|c_n| \leq Ar^n \qquad \text{for} \quad n = 0, 1, 2, \ldots$$

with some constant A independent of n.

Let us multiply $2R^k D_k$ to the both sides of (5) and sum up them with respect to k.

For the first sum involving $\{c_n\}$, we use $2|D_k D_{k+n}| \leq R^{-n/2} D_k^2 + R^{n/2} D_{k+n}^2$ to have

$$\sum_{k,n=1}^{\infty} R^k |D_k c_n D_{k+n}| \leq \frac{A}{2} \sum_{n=1}^{\infty} \left(\frac{r}{\sqrt{R}}\right)^n \sum_{k=1}^{\infty} (R^k D_k^2 + R^{k+n} D_{k+n}^2) \leq A_1 E$$

For the second sum, we have

$$\sum_{k,n=1}^{\infty} R^k|D_k L_k c_n D_n| \leq A \sum_{k=1}^{\infty}\left(\frac{R}{2}\right)^k |D_k| \sum_{n=1}^{\infty} r^n|D_n|$$

$$\leq A\left\{\sum_{k=1}^{\infty}\left(\frac{R}{4}\right)^k \sum_{n=1}^{\infty}\left(\frac{r^2}{R}\right)^n\right\}^{1/2} E \leq A_2 E.$$

The third sum containing $\{c_n\}$ is estimated as

$$\sum_{k,n=1}^{\infty} R^k D_k^2 |c_n L_n| \leq A_3 E.$$

For the sum of $kD_k L_{k-1} D_1$, we have

$$\sum_{k=1}^{\infty} kR^k|L_{k-1}D_k D_1| \leq 2|D_1| \sum_{k=1}^{\infty} (R^{k/2}|D_k|)\left(k\left(\frac{R}{4}\right)^{k/2}\right)$$

$$\leq 2|D_1| \left\{E \sum_{p=1}^{\infty} p^2\left(\frac{R}{4}\right)^p\right\}^{1/2} \leq A_4 E,$$

where A_1, A_2, A_3 and A_4 are constants depending only on r, A and R. To treat other sums, we estimate the cross terms $2|D_k D_j|$ $(j \neq k)$ by $4D_k^2+(1/4)D_j^2$. We have finally

$$\frac{d}{dt} E \leq \sum_{k=1}^{\infty} (C_0+kC_1+k^2C_2)R^k D_k^2,$$

where $C_2=(R^2-16)/(64N)<0$, C_0 and C_1 are independent of k and t. When k varies, $C_0+kC_1+k^2C_2$ has an upper bound B, with which (4) holds. The lemma is proved.

Remark. On the Banach space $L^1(0, 1)$ of all absolutely integrable functions on (0, 1), introduce a scalar product

$$(f, g)_R = \sum_{k=0}^{\infty} R^k L_k(f)\overline{L_k(g)}, \quad \text{where} \quad L_k(f) = \int_0^1 \left(x-\frac{1}{2}\right)^k f(x)dx.$$

Let H_R be the completion of $L^1(0, 1)$ with respect to the norm $\|f\|_R = \sqrt{(f, f)_R}$. Let H'_R be the vector space of all measurable functions $c(x)$ such that

$$\left|\int_0^1 c(x)f(x)dx\right| \leq \text{constant } \|f\|_R \qquad \text{for any } \ f \in L^1(0, 1).$$

A function $c(x)$ belongs to H'_R if and only if

$$c(x) = \sum_{n=0}^{\infty} c_n\left(x-\frac{1}{2}\right)^n \qquad \text{with} \sum_{n=0}^{\infty} R^{-n}|c_n|^2 < \infty.$$

(the proof omitted). We have proved that, if $c(x) \in H'_r$, the solution depends continuously on the initial value in the topology of H_R, where $0<r<R<4$.

§6. Construction of a solution

The idea is the following. We make the time variable discrete with mesh h in the equation (P.2) and delay the time in some of terms. This modification will be done in such a way that the total masses of approximative solutions be always equal to 1. So, the parabolic equation (P.2) is reduced to a series of linear ordinary differential equations. We have a family of functions which are piecewise linear in t. And we appeal to Ascoli-Arzelà theorem to obtain a sub-family converging to a solution.

Let us define at first a sequence of functions $\{u_n(x)\}_{n=0}^{\infty}$ depending on a positive parameter h such that

$$(1)\qquad (C+2Nsv'+2Nsm)h<1, \quad \text{where} \quad C=\operatorname{Max}\{|c(x)-c(y)|\,;\,0\leq x,\ y\leq 1\}.$$

Put $u_0(x)=\phi(x)$. Assume, by induction, that $u_n(x)$ has already been defined. Let us denote

$$(2)\qquad \xi_n=\int_0^1 xu_n(x)dx \quad \text{and} \quad c_n=\int_0^1 c(x)u_n(x)dx.$$

Let $u_{n+1}(x)$ be the absolutely integrable solution of the boundary value problem

$$(3)\qquad u_{n+1}-h\frac{d^2}{dx^2}\left\{\frac{x(1-x)}{4N}u_{n+1}\right\}+h\frac{d}{dx}[\{v'(1-x)-vx-sx(1-x)$$
$$+m(\xi_n-x)\}u_{n+1}]=\{1+h(c(x)-c_n)\}u_n, \quad \text{in} \quad (0, 1),$$

$$(4)\qquad \frac{d}{dx}\left\{\frac{x(1-x)}{4N}u_{n+1}\right\}-\{v'(1-x)-vx-sx(1-x)+m(\xi_n-x)\}u_{n+1}$$

tends to zero as $x\searrow 0$ or as $x\nearrow 1$.

Suppose, by induction, that

$$(5)\qquad u_n(x)\geq 0 \quad \text{and} \quad \int_0^1 u_n(x)dx=1.$$

Let us apply to get u_{n+1} the lemma in the next §7 with $f=\{1+h(c(x)-c_n)\}u_n$, $p=4N(v'+m\xi_n)$, $q=4N(v+m-m\xi_n)$, $r=2Ns$ and $\lambda=h/(4N)$, where $0<\xi_n<1$ because of (5). f is non-negative if (5) holds and if $Ch<1$, and the total mass of f is equal to 1. Therefore, we have one and only one solution u_{n+1} which is positive and of total mass 1, if $2Ns(v'+m)h<1$. So, (5) holds also for u_{n+1}. In this way, we can continue to define u_n's by induction on n if we assume (1).

Let $\{m_k(n)\}_{k=0}^{\infty}$ be the moment sequence of $u_n(x)dx$:

$$(6)\qquad m_k(n)=\int_0^1 x^k u_n(x)dx \qquad \text{for} \quad k=0, 1, 2,\dots$$

Multiplying x^k to the both sides of (3) and integrating over (0, 1), we have the recurrence formula

$$h^{-1}\{m_k(n+1)-m_k(n)\}+k\left(v+v'+s+m+\frac{k-1}{4N}\right)m_k(n+1)=$$
$$(7)\qquad =ksm_{k+1}(n+1)+k\left(v'+mm_1(n)+\frac{k-1}{4N}\right)m_{k-1}(n+1)+$$
$$+\int_0^1\int_0^1\{c(x)-c(y)\}x^k u_n(x)u_n(y)dxdy.$$

Since $0<m_k(n)\leq 1$ for all k and n, we have

$$(8)\qquad |m_k(n+1)-m_k(n)|\leq A_k h \quad \text{with} \quad A_k=C+k\left(v+v'+s+m+\frac{k-1}{4N}\right)$$

uniformly in h, where the relation $m_k<m_{k-1}$ is used.

Next, let us define a function $U(t, x, h)$ (piecewise linear in t) as follows

$$(9)\qquad U(t, x, h)=\left(\frac{t}{h}-n\right)u_n(x)+\left(n+1-\frac{t}{h}\right)u_{n+1}(x) \quad \text{if} \quad nh\leq t\leq (n+1)h.$$

Then $U(nh, x, h)=u_n(x)$ for all n, $U(t, x, h)$ is positive if $(t, x)\in(0, \infty)\times(0, 1)$ and the total mass of $U(t, x, h)$ is always equal to 1. Let $\{M_k(t, h)\}_{k=0}^{\infty}$ be its moment sequence. Then we have

$$(10)\qquad M_k(t, h)=\left(\frac{t}{h}-n\right)m_k(n)+\left(n+1-\frac{t}{h}\right)m_k(n+1) \quad \text{if} \quad nh\leq t\leq (n+1)h.$$

Moreover, (8) implies

$$(11)\qquad |M_k(t, h)-M_k(t', h)|\leq A_k|t-t'| \quad \text{if} \quad t\geq 0 \quad \text{and} \quad t'\geq 0.$$

Therefore, for each k, $\{M_k(t, h)\}$ is a family of uniformly bounded and equi-continuous functions of t depending on h as h is small. By the theorem of Ascoli-Arzelà, we can find a sequence $\{h_j\}$ (independent of k) tending to zero as $j\to\infty$ such that $M_k(t, h_j)$ tends (uniformly on each finite interval of t) to some continuous function $M_k(t)$ for all k. Since $\{M_k(t, h_j)\}_{k=0}^{\infty}$ is the moment sequence of probability Stieltjes measures on $[0, 1]$, the conditions (a) and (b) in §4 are satisfied. As $j\to\infty$, (a) and (b) are also true for $\{M_k(t)\}$. Therefore, at any t, $\{M_k(t)\}$ is the moment sequence of some probability Stieltjes measure $U(t, dx)$:

$$(12)\qquad M_k(t)=\int_0^1 x^k U(t, dx) \qquad \text{for} \quad k=0, 1, 2,\ldots$$

Note that, for any k,

$$(13)\qquad \int_0^1 c(x)x^k U(t, x, h_j)dx \longrightarrow \int_0^1 c(x)x^k U(t, dx) \quad \text{as} \quad j\longrightarrow\infty,$$

because $c(x)$ is assumed to be continuous on $[0, 1]$ so that $c(x)$ can be approximated uniformly by a sequence of polynomials. Putting $h=h_j$ in (7) and taking the limit as $j\to\infty$, we see that $\{M_k(t)\}_{k=0}^{\infty}$ satisfies the system of differential equations (2) in §4. Due to the lemma in §4, $U(t, dx)$ can be written as $U(t, x)dx$ and $U(t, x)$ is a solution of the problem (P). The assertion (i) of the theorem is proved.

Remark. Let us explain why we assume the continuity of $c(x)$ on $[0, 1]$. Assume, on the contrary, that $c(x)$ be merely bounded and Lebesgue measurable. Even in this case, we can choose a sequence $\{h_j\}$ (independent of k) such that the integrals on the left hand side of (13) converge to some finite number as $j\to\infty$. However, the Stieltjes integral on the right hand side of (13) may not be defined. This limit process may go well if $c(x)$ is bounded and Borel measurable.

§7. Lemma on ordinary differential equation

Let p, q, r and λ be given positive constants. Let us consider the solutions of the following ordinary differential equation (see (3)–(4) of §6)

$$
(1)\qquad \begin{aligned} &u-\lambda\frac{d}{dx}Bu=f \quad \text{in} \quad (0,1) \\ &\text{with} \quad Bu=\frac{d}{dx}\{x(1-x)u\}-\{p(1-x)-qx-2rx(1-x)\}u, \end{aligned}
$$

satisfying the boundary condition

$$
(2)\qquad Bu(x) \quad \text{tends to zero as} \quad x\searrow 0 \quad \text{or as} \quad x\nearrow 1.
$$

Given a f belonging to $L^1(0, 1)$, we shall find a solution u also belonging to $L^1(0, 1)$, where $L^1(0, 1)$ is the Banach space of all absolutely integrable functions on (0, 1).

Lemma. *There exists a positive number λ_0 (not smaller than $1/(pr)$) having the following property: if $0<\lambda<\lambda_0$ and if $f\in L^1(0, 1)$, the problem (1)–(2) has one and only one solution u in the space $L^1(0, 1)$ satisfying moreover the conditions* (3), (4) *and* (5) *below*:

$$
(3)\qquad \int_0^1 |u(x)|dx \le \int_0^1 |f(x)|dx \quad \textit{and} \quad \int_0^1 u(x)dx=\int_0^1 f(x)dx;
$$

(4) $x(1-x)u(x)$ *tends to zero as* $x\searrow 0$ *or as* $x\nearrow 1$;

(5) *if f is non-negative and not identically zero, u is everywhere positive in* (0, 1).

Proof. We introduce an auxiliary function

$$
W(x)=x^{1-p}(1-x)^{1-q}e^{rx}
$$

and put $\hat{u}=Wu$ (note that $B\{W^{-1}e^{-rx}\}=0$). If u is a solution of (1) with $f=0$, $\hat{u}$ satisfies the equation

$$
(6)\qquad \begin{aligned} &\left(x\frac{d}{dx}+p\right)\frac{d\hat{u}}{dx}=\frac{qx}{1-x}\frac{d\hat{u}}{dx}+F(x)\hat{u} \\ &\text{where } F(x)=\frac{(1/\lambda)+prx}{1-x}-pr+r^2x=\sum_{n=0}^{\infty} f_n x^n, \end{aligned}
$$

or equivalently, if we put $\xi=1-x$,

$$
(6')\qquad \begin{aligned} &\left(\xi\frac{d}{d\xi}+q\right)\frac{d\hat{u}}{d\xi}=\frac{p\xi}{1-\xi}\frac{d\hat{u}}{d\xi}+G(\xi)\hat{u} \\ &\text{where } G(\xi)=\frac{(1/\lambda)-pr\xi}{1-\xi}+qr+r^2\xi=\sum_{n=0}^{\infty} g_n\xi^n. \end{aligned}
$$

(6) or (6′) has two power series solutions

(7) $$\hat{u}_0(x)=\sum_{n=0}^{\infty} a_n x^n \quad \text{and} \quad \hat{u}_1(x)=\sum_{n=0}^{\infty} b_n(1-x)^n$$

where

$$a_0=1, \quad (n+1)(n+p)a_{n+1}=\sum_{k=0}^{n}(kq+f_{n-k})a_k, \quad n=0, 1, 2,\dots$$

$$b_0=1, \quad (n+1)(n+q)b_{n+1}=\sum_{k=0}^{n}(kq+g_{n-k})b_k,$$

$\hat{u}_0(x)$ and $\hat{u}_1(x)$ are absolutely convergent if $|x|<1$ or if $|1-x|<1$ respectively Note that $F(x)$ and $G(\xi)$ are power series with positive coefficients if $0<\lambda<1/(pr)$. So, there exists a constant λ_0 (not smaller than $1/(pr)$) such that all of $\{a_n\}$ and $\{b_n\}$ are positive if $0<\lambda<\lambda_0$. Hence, if $0<\lambda<\lambda_0$, $\hat{u}_0(x)$ is positive and strictly increasing, while $\hat{u}_1(x)$ is positive and strictly decreasing in (0, 1). Therefore, $\hat{u}_0$ and $\hat{u}_1$ are linearly independent and we have

(8) $$x(1-x)\left(\hat{u}_1\frac{d\hat{u}_0}{dx}-\hat{u}_0\frac{d\hat{u}_1}{dx}\right)=AW(x)e^{-rx},$$

where A is a positive constant.

If we put $u_j(x)=\hat{u}_j(x)/W(x)$ $(j=0, 1)$, they are linearly independent solutions of (1) with $f=0$. It is not difficult to see that

(9) $$Bu_0(0+)=Bu_1(1-)=0,$$

$$0<Bu_0(1-)\leq+\infty \quad \text{and} \quad 0>Bu_1(0+)\geq-\infty.$$

Thus, u_0 (resp. u_1) satisfies the boundary condition at $x=0$ (resp. $x=1$) but does not so at the other end point. This implies the uniqueness of the solution of (1)–(2).

Now, we define the Green function $K(x, y)$ and the Green operator K as follows

(10) $$K(x, y)=(\lambda AW(y))^{-1}e^{ry}u_0(\operatorname{Min}(x, y))u_1(\operatorname{Max}(x, y))$$

$$(Kf)(x)=\int_0^1 K(x, y)f(y)dy.$$

Kf makes sense if $f\in L^1(0, 1)$. Kf satisfies (1) and (2). The assertion (5) holds because $K(x, y)>0$. And, if $f\geq 0$, integrating the both sides of (1), we have the second equality of (3). This and $|Kf|\leq K|f|$ imply (3) for general $f\in L^1(0, 1)$. The proof of (4) is quite similar as that of (4) in §4. The lemma is established.

Acknowledgement. The author of the present paper is very grateful to Professor Takeyuki Hida for his kindness to suggest this problem.

DEPARTMENT OF MATHEMATICS
KYOTO UNIVERSITY

References

[1] M. Kimura, Diffusion model of intergroup selection, with special reference to evolution of an altruistic character, Proc. Nat. Acad. Sci. USA,. **80** (1983), 6317–6321, Genetics.

[2] D. V. Widder, The Laplace Transform. Princeton University Press, 1946.