AUTOROTATION, SELF-STABILITY, AND STRUCTURE OF SINGLE-WINGED FRUITS AND SEEDS (SAMARAS) WITH COMPARATIVE REMARKS ON ANIMAL FLIGHT

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I. INTRODUCTION

A samara is a winged fruit or seed that autorotates when falling. The functional significance of the samara is to reduce the falling speed of the diaspore, thus increasing the distance it may be transported by horizontal winds. The selection pressure behind its appearance thus is directed towards improvement of the dispersal potential of the plant. From the way the samara functions, it is obvious that its occurrence is restricted to tall plants (like trees), where some height can be spent on a rapid initial fall before the samara enters autorotation and thereby a slow descent.

Structurally samaras are relatively simple, and accordingly have evolved independently in a large number of plants. They range in size from the small, ca. 1 cm
long, samaras of some coniferous trees, to the *ca.* 18 cm long samara of the South American leguminous tree *Centrolobium robustum* Mart. (Ulbrich, 1928).

In autorotational descent the samara possesses self-stability. It furnishes an example of natural flight where stability is governed entirely by the structural pattern. Thus, the mechanics of stable, natural flight can be studied on samaras without the interference of the neuromuscular control as in animal flight.

The purpose of this investigation is to analyse the mechanics of the autorotational descent of samaras, with special reference to how stability is maintained. Thus aerodynamical, mechanical, and structural properties crucial for the inherent self-stability are pursued.

Although treated by Hertel (1966), calculations of induced air velocities (momentum theory) are included here, since they are of importance in calculating the relative air
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velocities at the blade in the strip analysis (blade element theory) performed in this paper.

The aerodynamics of samaras are in many respects similar to those of helicopters and autogyros. The simplified analysis performed in the paper is based partly on helicopter theory (McCormick, 1967; Shapiro, 1955), and most of the terms and symbols used conform to those used by McCormick and Shapiro (Text-fig. 1). Information on general aerodynamics can be found in such text-books as those by Jones (1942) or Abbott & von Doenhoff (1959).

Many factors discussed are of a general nature and apply also to the flight of animals. Comparisons with animal flight are made when appropriate throughout the paper.

Simple experiments on pitch stability were performed on thin, flat plates with various chordwise positions of the centre of mass. The performance of samaras of maple, Acer platanoides L., sycamore, Acer pseudoplatanus L., and spruce, Picea abies (L.) H. Karst., was studied from films (64 frames per sec) and from photographs. The latter were taken of samaras entering autorotation and when they were in stable autorotation. They were illuminated by 100 flashes per second (accuracy 1%) from a stroboscope (Brüel & Kjaer, 4910) and the camera shutter was kept open while the samaras descended, so that multiflash photographs were obtained.

There are few reports on autorotation of samaras, and to my knowledge there is none on stability.

Dingler (1889, with references to some older papers) made a classification of a large variety of air-dispersed plant diaspores according to their patterns of motion. One of his methods of tracing motion patterns of samaras was to drop them from various heights on to fine sand and read their attitude at impact from the impressions left on the sand. He also experimented with artificial samaras to find out the structures essential for autorotation, and here, as well as in tracing movements, arrived at correct conclusions. In his analysis of the mechanism of autorotation, however, he failed to put the various speed components together into resultant relative air streams at the blade, and so got a wrong idea about the mechanics of autorotation of samaras.

Ulbrich (1928), in his morphological description of fruits and seeds, followed Dingler's classification according to their patterns of movement. He illustrated a variety of samaras. Schmidt (1939) gave a short description of the movements of samaras. Hertel (1966, pp. 90–6) made performance measurements (sinking speeds) of a variety of samaras and calculated induced air velocities according to the momentum theorem. In his book, there are long-exposure photographs showing screw-shaped images of autorotating samaras. He also compared samaras with other high-drag objects.

II. RELATIVE AIR VELOCITIES

(1) Momentum theorem applied to the autorotating samara

The sinking speed of a samara in stable, vertical autorotation settles at that speed at which the vertical upward component of the total aerodynamic force becomes equal to the weight of the samara. Within the shaft of air passing through the swept disk, the airflow relative to the samara is retarded by the samara, which means that the air
in the shaft is accelerated downwards relative to the surrounding still air, the change of momentum furnishing the required thrust (\(=\) drag). Hence the velocity \(V_a\) of the air flowing through the swept disk, and the final velocity \(V_f\) of the air relative to the samara above the disk are smaller than the sinking speed \(V_s\) of the samara (Text-figs. 2, 3).

As in helicopter theory, some approximations regarding the pattern of air flow are made here, namely, (1) that the velocity is uniformly distributed over the whole disk area, and (2) that the air in the shaft is accelerated to half the maximum velocity \(\frac{1}{2}(V_s - V_f)\) before entering the disk from below, and accelerated further to the maximum velocity \(V_s - V_f\) after passing the disk. Thus the through-flow velocity \(V_d\) is considered

\[ V_f = \frac{V_s + V_f}{2} \]

through-flow velocity

\[ V_s = \text{sinking speed} \]

initial relative air speed = sinking speed

\[ \text{shaft of air passing through the disc of rotation of the samara} \]

Text-fig. 2. Movement of air relative to samara.

\[ V_s - V_f \]

maximum downward speed of air in the shaft

\[ \frac{V_s - V_f}{2} \]

induced speed at the disc of rotation

Text-fig. 3. Movement of air in the shaft relative to surrounding still air.
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to be the average of the sinking speed (= approach velocity) and the final air velocity relative to the samara

\[ V_d = \frac{V_s + V_f}{2}. \tag{1} \]

With these approximations the simple axial momentum theory may be applied to the samara. This theory has been applied to the autorotational descent of samaras, and to the hovering flight of humming-birds (Trochilidae), insects (Hertel, 1966, pp. 69, 75, 91), and the pigeon (Columbia livia Gmelin) (Pennycuick, 1968).

This is a simplified view of the flow pattern, which, however, has proved very useful in helicopter theory. Actually, the induced downward air velocity varies over the disk, the induced velocity being largest in concentric shells well out on the blade where the largest aerodynamic forces are elicited, as shown in Text-fig. 17.

The mass flow \( f_m \) in unit time through the swept disk is given by

\[ f_m = \rho A_d \frac{V_s + V_f}{2}, \tag{2} \]

where \( \rho \) is the air density, \( A_d \) is the horizontally projected area of the swept disk, \( V_s \) is the sinking speed of the samara = approach velocity of the air, \( V_f \) is the final velocity of the air relative to the samara above the disk, and \( \frac{1}{2}(V_s + V_f) \) is the through-flow velocity (equation (1)).

The still air entering the shaft from below is eventually accelerated to a maximum velocity (behind, above, the samara) of \( V_s - V_f \), and the rate of change of momentum, which equals the weight \( W \), is

\[ W = f_m(V_s - V_f) = \rho A_d \frac{V_s + V_f}{2} (V_s - V_f), \tag{3} \]

which can be written

\[ \frac{W}{A_d} = \rho \frac{V_s + V_f}{2} (V_s - V_f) = \rho \frac{1}{2} (V_s^2 - V_f^2), \tag{4} \]

where \( W/A_d \) is the disk loading.

From equation (4) the following proportionality can be found

\[ V_s \propto \sqrt{\frac{W}{A_d}}. \tag{5} \]

Thus, other things being equal, the sinking speed of a samara is proportional to the square root of its disk loading. The same relation holds for hovering animals of any size, with the modification that it is the air flowing through the wing disk that is accelerated to a final velocity (below the animal) proportional to the square root of the disk loading. The characteristic flight speeds of animals, of any size, in horizontal flight are roughly proportional to the square root of the respective wing loading (Pennycuick, 1968).
(2) Relative air velocities in vertical autorotational descent

Throughout this paper by vertical descent is meant vertical descent relative to the ambient air. Thus, vertical descent relative to the ambient air may prevail even if the descent path is oblique relative to the vertical because of horizontal winds.

The direction and velocity of the relative air stream differ at every point along the span of the samara. The resultant velocity is composed of various velocity components.

At the centre of rotation the resultant relative air stream is vertical (axial) and meets the samara from below. Its velocity $V_d$ is equal to the through-flow velocity (equation (1)), or the sinking speed $V_s$ minus the induced speed at the disk

$$V_d = V_s - \frac{V_a - V_f}{2} = \frac{V_s + V_f}{2}. \quad (6)$$

At the blade the vertical through-flow velocity is the same as at the centre of rotation, $V_d$. In an analysis of forces and relative air velocities at a blade element, the velocities are resolved into spanwise components and components lying in a plane normal to the span axis. Since the blade is set at an angle, coning angle $\beta$, to the tip path plane, the axial through-flow is not normal to the blade span. Thus the through-flow velocity is resolved into a spanwise component $V_{ds}$ ($V_{ds} = V_d \sin \beta$) (Text-fig. 4), the aerodynamic significance of which is negligible (Shapiro, 1955, p. 29), and into a component $V_{dn}$ normal to the blade span (Text-fig. 4)

$$V_{dn} = V_d \cos \beta. \quad (7)$$

In addition, there is a tangential velocity component $V_t$ due to rotation of the samara

$$V_t = \omega r_n, \quad (8)$$
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Text-fig. 5. Vertical autorotational descent. Relative air velocities in a plane normal to the span axis (pitching plane).

Text-fig. 6. Diagram showing how the relative air velocity of a samara in autorotational descent with side-slip is resolved into components normal to and parallel to the tip path plane.

where \( \omega \) is the angular velocity in radians/sec \( (\omega = 2\pi f, f = \text{revolutions/unit time}) \) and \( r_n \) is the radial distance from (normal to) the axis of rotation to the blade section. The normal velocity component \( V_{dn} \) and the tangential velocity component \( V_t \) of the blade section together constitute the resultant relative air velocity \( V_{\text{res}} \). Since \( V_{dn} \) and \( V_t \) are normal to each other,

\[
V_{\text{res}} = \sqrt{(V_{dn}^2 + V_t^2)}.
\]

Combination with equations (7) and (8) gives

\[
V_{\text{res}} = \sqrt{[(V_{dn}\cos\beta)^2 + (\omega r_n)^2]}.
\]

Thus, the farther out from the centre of rotation the blade element is located, the more horizontal the resultant relative air stream and the larger its velocity (Text-fig. 5).

(3) Relative air velocities in autorotational descent with side-slip

If the disk of rotation tips side-ways, side-slip will occur in the direction of the low side. The descent path of the samara in still air thus deviates from the vertical. The
resultant relative air velocity of the (whole) samara is resolved into one axial (through-flow velocity) component, $V_{d, \text{slip}}$, parallel to the axis of rotation, and one component, $V_{\text{slip}}$, parallel to the tip path plane (Text-fig. 6). The through-flow velocity, $V_{d, \text{slip}}$, is different from $V_d$ in vertical descent and is not constant since side-slip is a transient condition. The absolute magnitude of $V_{d, \text{slip}}$ is not considered here.

The azimuth angle $\psi$ is the angle between the direction of side-slip and the span axis of the samara as projected on the tip path plane, measured from downwind position, in direction of rotation, as shown in Text-figs. 1 and 7.

The relative air velocity at the blade due to side-slip is resolved into a spanwise component, which may be neglected, and into two components lying in planes normal to the span axis of the blade. The latter two components contribute to the resultant...
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Relative air velocities at the blade. The effect of the velocity component, $V_{\text{slip}}$, parallel to the tip path plane, on the local relative air velocities at a blade section varies with the azimuth angle $\psi$.

The total tangential relative air velocity, $V_{t, \text{slip}}$, at a blade section is given by

$$V_{t, \text{slip}} = V_t + V_{\text{slip}} \sin \psi,$$

where $V_t$ is the tangential velocity due to rotation of the samara, and $V_{\text{slip}} \sin \psi$ is a velocity component due to side-slip (Text-fig. 7). This second velocity component is positive on the side of advance ($0° < \psi < 180°$), negative on the side of retreat ($180° < \psi < 360°$).

$V_{\text{slip}}$ also gives a radial velocity component parallel to the tip path plane and equal to $V_{\text{slip}} \cos \psi$ (Text-fig. 7). Since the samara takes up a coning angle $\beta$, $V_{\text{slip}} \cos \psi$ is resolved into a spanwise component, which is without significance, and a component equal to $V_{\text{slip}} \cos \psi \sin \beta$, which is normal to the span axis and parallel to a plane through the span axis of the samara and its axis of rotation (Text-fig. 8).

The total relative air velocity, $V_{dn, \text{slip}}$, normal to the span axis and parallel to a plane through the span axis of the samara and its axis of rotation (Text-fig. 8) is given by

$$V_{dn, \text{slip}} = V_{dn, \text{slip}} \cos \beta + V_{\text{slip}} \cos \psi \sin \beta.$$

The last velocity component is positive on the leading half of the swept disk ($90° < \psi < 270°$), negative on the trailing half ($270° < \psi \leq 360°$ and $0° \leq \psi < 90°$).
Text-fig. 9. Autorotational descent with side-slip. Relative air velocities (tangential, perpendicular, and resultant) in a plane normal to the span axis (pitching plane). The illustrated relation between the tangential and perpendicular components $V_{\text{slip}} \sin \psi$ and $V_{\text{slip}} \cos \psi \sin \beta$ respectively, due to side-slip is that for a coning angle, $\beta$, of 20°. The tangential and perpendicular velocity components, due to side-slip are positive, equal to zero, or negative depending on the azimuth angle, $\psi$. They are added to the velocity components due to rotation and axial descent, respectively. The resultant velocities are constructed for $0^\circ$, $90^\circ$, $180^\circ$ and $270^\circ$ azimuth. Lower diagram illustrates how the resultant relative air velocity in side-slip, $V_{\text{res, slip}}$, oscillates about the resultant velocity, $V_{\text{res}}$ with no side-slip velocity components added, as the azimuth angle varies. Diagram based on the same relations between various velocity components as in upper diagrams. The upper and lower diagrams drawn to somewhat different scales.

The resultant relative air velocity, $V_{\text{res, slip}}$, in a plane normal to the span axis of a samara in autorotational descent with side-slip (Text-fig. 9), is given by the following equation (in analogy to equation (9) which applies to vertical descent without side-slip)

$$V_{\text{res, slip}} = \sqrt{[(V_d, \text{slip} \cos \beta + V_{\text{slip}} \cos \psi \sin \beta)^2 + (V_t + V_{\text{slip}} \sin \psi)^2]}.$$  

The radial distance from the centre of rotation enters the above equation via $V_t$ which equals $\omega r_n$ (equation (8)).
III. STABILITY

In static stability only the forces and moments set up after a disturbance from the equilibrium state are considered. In a statically stable system a disturbance from the equilibrium results in forces tending to move the system back towards the equilibrium state.

In dynamic stability the movements following a disturbance from the equilibrium state are considered. A dynamically stable system eventually returns to the equilibrium state, either gradually or after oscillations of decreasing amplitude. A dynamically stable system is also statically stable. But a statically stable system may be dynamically unstable, namely if the restoring forces lead to oscillations of increasing amplitudes about the equilibrium state.

A samara is free to move in any sense. In autorotational descent it possesses both static and dynamic stability. Thus, after a disturbance from the equilibrium state, the samara tends to return to the equilibrium state and remain there. Mainly it is the static stability of samaras in autorotation that is considered in this paper.

The ways in which stability is maintained in various planes and angles of an autorotating samara (Text-fig. 1) will be dealt with in the following order:

(1) Stability in the pitching plane = feathering plane, involving stability of the angles of attack and the gliding angles. It is governed by the chordwise mass distribution and profile shape of the blade.

(2) Stability in the coning plane = flapping plane, involving stability of the coning angle.

(3) Stability of the angle of the tip path plane relative to the horizontal, involving directional stability.

(1) Stability of the angles of attack of the blade

The pitching angle (blade or feathering angle) as used in this paper is defined as the angle between the chord of the blade and a tangent plane to the conical surface swept by the samara blade. The pitching plane is normal to the span axis of the samara (Text-fig. 1).

In this qualitative analysis of the stability of samaras, all aerodynamic forces on the samara are represented as one single, resultant air force acting through the chordwise centre of pressure, c.P., which is so located that the pitching moment (the moment in the nose-up and nose-down sense) caused by the resultant force is the same as that of the distributed forces. The centre of pressure as defined here means the centre of all aerodynamic forces, pressure forces as well as friction forces.

The samara blade is essentially a flat plate operating at Reynolds (Re) numbers of about 2000 (in Acer).

It can easily be demonstrated that a flat plate, operating at a Re number of about 2000, possesses dynamic stability in the pitching plane as long as its centre of mass, c.M., lies between ca. 27 % and ca. 35 % of the chord length behind the leading edge. When falling, it enters a glide path and takes up an angle of attack and a gliding angle which are both determined by the chordwise c.M. position. The farther back the c.M.,
the larger the angle of attack and the steeper the glide path. The force of gravity acting at the plate’s c.m. and the aerodynamic force interact in such a way as to give pitch stability.

In the case of samaras it is not only the force of gravity, but also the centrifugal force of the blade that interact with the aerodynamic force to give pitch stability as described below. Hence, as regards pitch stability, the centrifugal force of a samara in autorotation is the functional analogue to the force of gravity of a flat plate in a straight glide.

Because of the coning angle $\beta$, the centrifugal force, acting normal to the axis of rotation, tends to lay the samara blade parallel to the tip path plane. For analysis of this effect, the centrifugal force is resolved into a spanwise component and a perpendicular component, $C_{d,\text{perp}}$, which is perpendicular to the span axis and lies parallel to a plane through the span axis of the samara and its axis of rotation (Text-figs. 10, 13). The centrifugal force of a strip acts through the chordwise c.m., the position of which is constant at various angles of attack. However, as the angle of attack varies, there is a fore-and-aft movement of the c.p. Since the chordwise c.m. of a blade lies within the range of potential movement of the c.p., these centres coincide at a particular angle of attack. When they do, the strip is in equilibrium in the pitching plane (Text-fig. 10A).
Because of the manner the c.P. moves with changing angles of attack, this equilibrium is a stable one.

As the angle of attack becomes larger than the equilibrium one, the c.P. moves aft of the c.M., the resultant aerodynamic force and the perpendicular component of the centrifugal force then forming a couple, tending to restore the equilibrium angle of attack (Text-fig. 10B). On the other hand, when the angle of attack becomes too small, the c.P. moves ahead of the c.M. (Text-fig. 10 C), and so the angle of attack is increased again.

This c.P. movement renders the samara statically stable in pitch. It is also dynamically stable in pitch and probably performs damped pitching oscillations upon a disturbance. The pitching oscillations (distinguished in dynamic stability theory) following a disturbance are of two kinds. One is connected with variations of the angle of attack, as described in this section, and is called 'the short-period oscillation'. The other is 'the long-period or phugoid oscillation', due mainly to variations of the speed (Weyl, 1945a). The variation of forces upon changes in horizontal and sinking speed is dealt with in Section III (2).

The torsion axis of a samara is approximately the span axis best fitting the c.M. of all chordwise strips of the samara (Text-fig. 16). For stability to be maintainable, the c.M. must lie well behind the most forward potential position of the c.P., so that a reduction of the angle of attack below the equilibrium one can be counteracted (Text-fig. 10 C). In samaras the c.M. lies about one-third chord length behind the leading edge, which is well behind the most forward potential position of the c.P.

The chordwise position of the c.M. of strips of the blade gives the samara an inherent pattern of local angles of attack along the blade. If the blade is relatively flat, either side may be turned upwards and the samara thus may rotate in either direction.

Since the local angles of attack are different along the samara span as a result of different tangential speeds, the equilibrium condition shown in Text-fig. 10 A does not apply to all strips. The angle of attack is large near the base of the samara (nearly 90° at the centre of rotation, Text-fig. 5) and decreases towards the blade tip. This means that the c.P. is located near the mid-chord point proximally, near the 25% chord point distally. Hence there is a nose-down pitching moment proximally and a nose-up pitching moment distally. The actual pitching angle taken up by the blade is a compromise between the inherent equilibrium angles of different strips. The distal part of the blade dominates in determining the pitching angle because of its relatively large aerodynamic forces. The over all effect, as averaged over the whole blade, is that illustrated in Text-fig. 10.

Schmitz (1960, pp. 87, 110) gave data on c.P. movements of flat plates at Re numbers of 42,000–420,000, leading to stability of the angle of attack by a similar mechanism to that outlined above for samaras. Best stability in this Re region was obtained with a c.M. position 25–30% of the chord length behind the leading edge.

The kind of movement of the c.P. described above, ordinarily does not apply to aircraft wings or helicopter rotor blades, which operate at much higher Re numbers. Aircraft wings and rotor blades with symmetrical profiles have a stable c.P., whereas asymmetrical profiles (those having one side more curved than the other) ordinarily
have a c.p. movement which is the reverse of that of samaras, giving instability in the pitching plane (e.g. Jones, 1942, p. 71).

(2) Stability of the gliding angles of blade sections

The direction of the aerodynamic force of an aerofoil depends on the aerofoil profile and its angle of attack. It is customary to express the direction of the resultant force as the ratio between its two component forces, lift and drag. Lift is a force component normal to the direction of the resultant relative air stream, whereas drag is a force component in the direction of this stream. In a lift-producing aerofoil, lift is the useful force, whereas drag is a non-useful force. One measure of the efficiency of an aerofoil thus is the lift/drag ($L/D$) ratio.

The gliding angle is the angle between the glide path and the horizon. The equilibrium gliding angle $\epsilon$ is strictly determined by the $L/D$ ratio (Text-fig. 12) such that

$$\cot \epsilon = \frac{L}{D}. \quad (14)$$

In equilibrium gliding the resultant force is directed vertically upwards and balances the weight.

The samara as a whole descends vertically, and thus produces only drag. But this drag of the whole samara disk owes its origin to the lift and drag forces on the blade.

In samaras, strips at different spanwise locations have different $L/D$ ratios (because of different angles of attack) and thus different natural gliding angles. The $L/D$ ratio is large in the outer parts of the blade, whereas it is small in the inner parts due to large angles of attack. Hence the lift and drag coefficients vary along the blade as a consequence of various angles of attack. The closer to the centre of rotation, the more vertical the relative wind (Text-fig. 5) and thus the drag force, which here gives a contribution in a useful direction, i.e. upwards. But because of the relatively low speeds near the centre of rotation, the drag force is relatively small. The gliding angle actually taken up by a samara blade section is the result of a compromise between the natural gliding angles of various strips (determined by the local $L/D$ ratio). Therefore the resultant aerodynamic force of some strips may be inclined somewhat backwards and that of others somewhat forwards. But the various horizontal components cancel out, so that the resultant aerodynamic force of the whole samara lies on a vertical plane through the span axis. Again the distal part of the blade dominates in determining the gliding angle because of its relatively large aerodynamic forces.

In the following analysis of stability of the gliding angle, only one strip near the spanwise centre of pressure is considered, and the resultant aerodynamic force of the entire samara is considered to act on this strip (Text-fig. 11).

If the gliding path becomes steeper than the natural one (Text-fig. 11 A), there will be a nose-down rotation of the blade about its span axis since the angle of attack is automatically maintained constant (as outlined in the foregoing section). The angle $(90^\circ + \epsilon - \alpha)$ between the section chord and the resultant aerodynamic force, $R$, is constant (being determined by the blade profile and the angle of attack). Thus, after a nose-down rotation $R$ becomes inclined forwards, giving a forward propulsive component $R_h$ that increases the horizontal speed, i.e. speeds up rotation of the samara
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Text-fig. 11. Diagram of a chordwise blade section showing how the profile gliding angle near the spanwise C.P. is maintained constant by tilting of the total aerodynamic force $R$, leading to speed change, after a disturbance from the equilibrium state $A$. The horizontal line in the figure is the tangential plane to the swept cone, and the pitching angle is the angle between this plane and the blade chord. The angle of attack $\alpha$ and the angle $(90^\circ + \epsilon - \alpha)$ between the section chord and the resultant force $R$ are kept constant in the figures. The gliding angle is the variable. For simplicity the magnitude of the resultant force $R$ is kept constant in the three cases illustrated. The figure applies also to the wings of any gliding animal. Provided that the gliding path is straight and the wing span horizontal, the horizontal line in the figure then corresponds to horizon.

(Text-fig. 11B). This leads to a more horizontal relative air stream followed by a nose-up rotation of the blade section (so as to maintain the angle of attack constant) until $R$ is again on a vertical plane through the span axis.

On the other hand, by the same mechanism, a more shallow gliding angle than the natural one results in $R$ being tilted backwards, thus giving a backward component $R_h$. The resulting decrease in horizontal speed, i.e. slow down of rotation of the samara, brings about a more vertical relative air stream, and so there is a nose-down rotation until $R$ lies on a vertical plane through the span axis.
The automatic adjustment of the relative air speed such that the vertical component of the resultant force $R$ equals the weight $W$ of the samara, is accomplished by way of pitch angle adjustments. The regulation of gliding angle and the regulation of speed are thus interrelated.

If the relative air velocity is too small to make the vertical component of $R$ equal to $W$, the excess vertical downward force will accelerate the samara downwards. This results in the situation illustrated in Text-fig. 11B, and so $R_h$ will speed up the horizontal speed. As outlined above, the blade will then settle in its natural gliding angle so that $R$ lies on a vertical plane through the span axis, and the relative air speed will be such that the vertical component of $R$ is equal to $W$.

If the relative air velocity is too high, so that the vertical component of $R$ is larger than $W$, the downward speed will decrease. This results in the situation illustrated in Text-fig. 11C, and so the horizontal, i.e. tangential, speed slows down too. In analogy to the foregoing discussion, the blade will eventually settle in its natural gliding angle so that $R$ lies on a vertical plane through the span axis and the relative air speed is such that the vertical component of $R$ is equal to $W$.

At given pitching and coning angles, the relative air velocities at the blade must reach certain values to make the vertical component of the resultant aerodynamic force equal to the weight of the samara.

The larger the part that the tangential velocity contributes to the resultant relative air velocity $V_{res}$, the smaller the sinking speed of the samara. The perpendicular component of the through-flow velocity is a function of the sinking speed of the samara (equations (6) and (7)). The relation between the tangential velocity $V_t$ and the
perpendicular component $V_{dn}$ of the through-flow velocity is determined by the $L/D$ ratio such that

$$
\frac{V}{V_{dn}} = \frac{L}{D}.
$$

Thus, other things being equal, the larger the $L/D$ ratio, the higher the speed of rotation and the slower the rate of sink of the samara (Text-fig. 12).

Since the $L/D$ ratio and the inherent gliding angle of the blade vary along the blade because of different local tangential velocities and thus angles of attack, the natural gliding angle of a samara in autorotation is difficult to define. Another non-dimensional coefficient giving some measure of samara blade efficiency is the ratio between the (horizontal) tangential speed of the tip and the sinking speed of the samara. These data are easily collected. This ratio is determined by the blade's $L/D$ ratio, but is not equal to it, and may be influenced also by the disk loading. This ratio can be expressed also as the tip path angle relative to horizon.

The gliding path of a samara blade is a narrow helix. But the discussion of the automatic adjustment of gliding angle and gliding speed according to the $L/D$ ratio and weight applies also to straight glide paths of any gliding object. In some insects, birds, and bats the wings may be unstable in the pitching plane because of unstable C.P. movements (opposite to those of samaras upon changing angles of attack). In such cases stability in the pitching plane is accomplished by the tail or by neuromuscular control, such that a certain angle of attack is maintained. The equilibrium gliding angle and gliding speed corresponding to a certain angle of attack are then adjusted as outlined above.

(3) Stability of the coning angle

The coning angle taken up by the samara is determined by opposing moments set up by centrifugal and aerodynamic forces. The centrifugal force, $C$, of a strip is determined by the mass $M$, tangential velocity $V_t$, and the radius $r_n$ from the axis of rotation to the strip, such that

$$
C = \frac{MV_t^2}{r_n}.
$$

Since $V_t = \omega r_n$,

$$
C = M\omega^2 r_n.
$$

The magnitude and spanwise distribution of the centrifugal forces of the proximal end of the samara and of the blade may be calculated in analogy to the calculation of the magnitude and spanwise distribution of the pressure (p. 590). For such an analysis, strips of the samara must be weighed, and the corresponding tangential velocities and radii measured (the radii normal to the axis of rotation). The total centrifugal force of the blade is equal to the centrifugal force of the total mass of the blade when concentrated at the spanwise C.M. of the blade (Shapiro, 1955, p. 153). A corresponding relation applies to the part of the samara proximal to the centre of rotation. The spanwise points of action of the resultant centrifugal forces when giving the same moment as the distributed centrifugal forces (centre of percussion), may be
calculated in analogy to the calculation of the position of the spanwise c.P. (see Section V).

In Text-fig. 13 the centrifugal forces are represented as two resultant forces, one proximal $C_p$, and one distal $C_d$. Since the centre of rotation approximately coincides with the c.m. of the samara, the opposing centrifugal forces on both sides of the centre of rotation are of the same magnitude.

When the coning angle varies, the angular velocity $\omega$ changes so that the vertical component of the resultant aerodynamic force remains equal to the weight of the samara. This affects the centrifugal forces (equation (17)). However, for small changes in coning angle when the coning angle is relatively small, the approximation is adopted, that the angular velocity and the radial distances to the centres of the centrifugal forces are constant. In fact, they change relatively little with changes of the coning angle when this is small as in equilibrium descent. From this approximation it follows that the centrifugal forces are considered to remain constant for small changes of the coning angle.

The centrifugal forces act on the moment arms $P_p$ and $P_d$ (Text-fig. 13). These arms vary with the coning angle according to

$$P_p = r_{cpp} \tan \beta,$$

and

$$P_d = r_{cdd} \tan \beta,$$

where $r_{cpp}$ and $r_{cdd}$ are the radii to the two centres of the centrifugal forces.

The centrifugal moments tend to reduce the coning angle. The sum of the centrifugal moments, $\tau_c$, about the centre of rotation is

$$\tau_c = C_p r_{cpp} \tan \beta + C_d r_{cdd} \tan \beta,$$

where $C_p$ and $C_d$ are the centrifugal forces.
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In equilibrium descent the vertical component of the total aerodynamic force is equal to the weight $W$ of the samara. The resultant force thus is $W/\cos\beta$ (Text-fig. 13). Its moment $\tau_a$ about the centre of rotation is

$$\tau_a = \frac{W}{\cos\beta}r_{cp},$$

(20)

where $r_{cp}$ is the spanwise distance to the c.p. This moment tends to increase the coning angle. At equilibrium the moments cancel out

$$\tau_c = \tau_a,$$

$$C_p r_{cp} \tan\beta + C_d r_{oed} \sin\beta = \frac{W}{\cos\beta}r_{cp},$$

(21)

As the equilibrium coning angle is relatively small, the sum of the moments produced by the centrifugal forces changes rapidly upon a change of coning angle (the lever arms $P_p$ and $P_d$ being tangent functions of the coning angle, left side of equation (21)), whereas the opposing moment of the aerodynamic force changes slowly upon a change of coning angle (the force being an inverse cosine function of the coning angle, right side of equation (21)). Thus it is essentially the moments produced by the centrifugal forces that change upon a change of coning angle until the centrifugal and aerodynamic moments $\tau_c$ and $\tau_a$ cancel out at the equilibrium coning angle.

The higher the $L/D$ ratio, the larger the part that the tangential velocity contributes to the resultant relative air velocity (equation (15)), and the smaller the coning angle, since the centrifugal force (tending to reduce the coning angle) increases with the angular velocity squared (equation (17)). The aerodynamic force increases with the resultant speed squared, which, however, remains nearly constant upon small changes of coning angle, being determined by the weight of the samara.

At equilibrium the moments about the c.m. cancel out, as do the vertical forces (both the upward and downward ones are equal to the weight of the samara). The opposing, horizontal, centrifugal forces cancel out. But there remains one horizontal force, namely the horizontal component, $W\tan\beta$ (Text-fig. 13), of the resultant aerodynamic force. It tends to accelerate the samara blade proximally. But its direction of action varies rapidly as the samara rotates, so its effect is negligible.

Photos were taken of autorotating samaras of Acer platanoides, A. pseudoplatanus and Picea abies which had the c.m. marked with a white spot. Constant light was used, and the shutter was kept open as the samaras descended. In the screw-shaped traces obtained, the path of the white-marked c.m. was almost linear.

The smaller the coning angle, the larger the perpendicular component of the through-flow velocity, $V_{da}$, and the closer to vertical the resultant aerodynamic force. Therefore, the smaller the coning angle, the slower the rate of sink of the samara.

(4) Directional stability

In this section on directional stability is considered the stabilizing mechanism by which the tip path plane is restored to the horizontal after a disturbance, whereby a vertical descent path relative to the ambient air is maintained.
In vertical autorotational descent the resultant aerodynamic force as averaged over a whole number of revolutions is coincident with the axis of rotation. Upon tilting of the tip path plane, the resultant aerodynamic force will be tilted towards the low side. Then side-slip in the direction of the low side will start. Side-slip has different effects on the resultant relative air speed at the samara depending on its azimuth position. Directional stability is governed by the effect of the side-slip velocity. (See Section II(3) and Text-figs. 6–9.)

The contributions from the side-slip velocity to the relative air velocities at the samara are analysed by resolving the relative side-slip velocity into a spanwise component that may be neglected, and two components lying in planes normal to the span axis (pitching plane). Of the latter two, the one parallel to the tip path plane is the most important one, \( V_{\text{slip}} \sin \psi \). It reaches a positive maximum at \( \psi = 90^\circ \), and a negative maximum at \( \psi = 270^\circ \). The other, perpendicular, component, lying in a plane through the span axis of the samara and its axis of rotation, is much smaller, \( V_{\text{slip}} \cos \psi \sin \beta \). Its magnitude variation is phase-lagged \( 90^\circ \) to that of the component parallel to the tip path plane. These components due to side-slip are added to the components due to rotation and axial descent respectively. If the two sums are squared, then added and the square root taken, the resultant relative air velocity, \( V_{\text{res, slip}} \), in a plane normal to the span axis is obtained (equation (13), Text-fig. 9).

Since the perpendicular component of side-slip is small relative to the other, the resultant air velocity, \( V_{\text{res, slip}} \), reaches its maximum at an azimuth only a little larger than \( 90^\circ \), and its minimum after a further \( 180^\circ \), or at an azimuth a little larger than \( 270^\circ \) (Text-fig. 9). Other things being equal, the aerodynamic force of the blade varies with the square of the resultant relative air velocity. But as the velocity of the resultant relative air stream changes due to side-slip, also the direction of incidence of the relative air stream changes over one revolution, such that the relative air stream at the blade is more horizontal when the blade is in rear and advancing positions, more vertical when the blade is in front and retreating positions (Text-fig. 9). Hence the angle of attack tends to vary with azimuth of the blade. Since the blade automatically adjusts to its inherent angle of attack, the pitching angle of the blade tends to vary with azimuth, i.e. the blade tends to rotate in the nose-up and nose-down sense about its torsion axis. As long as side-slip occurs there is a tendency to this cyclic variation of pitch angle during every revolution of the samara about its c.m. Because of inertial forces about the torsion axis, there is a delay in adjustment of the angles of attack. However, it is uncertain whether the pitching moments are large and long-lasting enough to cause any essential variations of pitch angle. If not, the pitch angle taken up will be an average one. Since the aerodynamic forces vary also with the angle of attack, the variation in magnitude of the resultant aerodynamic force of the blade is somewhat phase-lagged to the variation of the relative air velocity, i.e. the maximum upward tilting moment will occur at an azimuth somewhat larger than \( 90^\circ \).

Because of its rotation the samara functions as a gyro. Therefore the tilting moment applied to the rotating samara, due to side-slip, results in a tilting of the tip path plane after a phase lag of \( 90^\circ \) relative to the region of action of the moment. Thus a maximum upward tilting of the swept disk will occur near its lowest point at an azimuth some-
what larger than $180^\circ$, i.e. somewhat after the blade tip has passed the lowest point of its path. Hence the tip path plane tends to be restored to the horizontal and the samara to a vertical descent path.

In some samaras, however, the moment, due to side-slip, on the tip path plane has a tendency to result in tilting in new directions, such that the lowest point of the tip path shifts in the direction opposite to the direction of rotation of the samara. The reason for this probably is that the maximum upward tilting moment then occurs at an azimuth substantially larger than $90^\circ$ (possibly around $180^\circ$). This may be so because (1) the resultant velocity reaches its maximum at an azimuth somewhat larger than $90^\circ$ (due to the perpendicular component, $V_{\text{slip}} \cos\psi \sin\beta$, Text-fig. 9), and because (2) the angles of attack are larger at azimuths between $180^\circ$ and $270^\circ$ than at azimuths between $0^\circ$ and $90^\circ$ (Text-fig. 9, top right) (due to the perpendicular component $-V_{\text{slip}} \cos\psi \sin\beta$—of the side-slip velocity and possibly to delay in adjustments of the angles of attack because of inertial forces about the torsion axis of the blade). Due to gyroscopic action a point somewhere around $270^\circ$ will come highest (a point at an azimuth of $90^\circ$ more than the azimuth where the maximum upward tilting force acts) and a point around $90^\circ$ will come lowest.

Side-slip follows in the changing directions of the lowest point of the tip path, and so the C.M. of the samara (i.e. the whole samara) tends to move in a helical path opposite to the direction of rotation of the samara about its C.M. After a disturbance, some samaras enter this circling movement in the direction opposite to its direction of rotation. In some cases this leads to a break down of autorotation and a rapid fall. However, most samaras possess very good dynamic stability, and after a disturbance, leading to tip path tilting and subsequent side-slip, the tip path plane is rapidly restored to the horizontal and the samara returned to a vertical descent path.

IV. ENTRANCE INTO AUTOROTATION

When a samara is dropped with its C.M. first and its blade directed strictly upwards, the samara usually needs a high fall before entering autorotation, or it may fail to rotate at all. When falling with its C.M. first and with the flat blade trailing, there is no lateral, inertial force at the blade which is a prerequisite for autorotation to occur.

If the blade is somewhat bent, twisted, or if its trailing edge is undulated, the samara usually settles into autorotation more rapidly, probably because lateral aerodynamic forces on the irregular blade induce a circular path of the blade tip, whereby centrifugal forces are set up. Once centrifugal forces act through the chordwise C.M. of the blade, the samara rapidly adjusts its attitude to the inherent section angles of attack, section gliding angles, and coning angle.

Many samaras are attached to the plant with the long axis near to the horizontal or with the C.M. higher than the blade. When shed, they rapidly settle into autorotation.

When falling (with the blade in other positions than trailing), the samara blade swings through or near a trailing position, whereupon the blade tip enters a helical path. Once the tip has entered a helical path, the coning angle is rapidly reduced, the speed of rotation is increased, and the rate of sink is strongly reduced. In the Acer
Text-fig. 14. Diagram illustrating entrance into autorotation. (A) Beginning of fall with the blade almost horizontal. Because of resistance from the air, the blade will swing upwards towards a trailing position behind the C.M. of the samara. Inertial forces due to angular acceleration of the blade tend to oppose the swing. (B) and (C) As a consequence of the force of gravity and of the inertial forces (the resultants of which act at the blade's mass axis, cf. Text-fig. 16) the blade (section a-a) will adjust to its inherent angles of attack, and so the lift component $L$ of the total aerodynamic force $R$ initially will be horizontal, leading to rotation about the C.M. This results in centrifugal forces and a more horizontal relative wind at the blade, and so the pitching angle and the coning angle of the samara adjust to the equilibrium values (cf. Text-figs. 11 B, 13).

In Pl. 1 A the coning angle was reduced from ca. $70^\circ$ to ca. $17^\circ$ in $\frac{8}{100}$ sec. The sequence of events leading to autorotation probably is as follows:

Two forces are of importance for the start of autorotation: (1) the force of gravity, and (2) inertial forces due to angular accelerations of the blade. The action of these two forces is similar and their effects additive.

(1) When the samara starts falling with its blade in an inclined position, the resultant
force of gravity of a section (as section $a-a$ in Text-fig. 14) acts through the C.M. of that section. Because of the force of gravity on the blade, and because the section C.M. lies ca. one-third of the blade chord behind the leading edge, the section tends to adjust to its inherent angle of attack. Hence the aerodynamic force is initially inclined laterally as in Text-fig. 14C. Since the blade’s C.P. lies lateral to the C.M. of the samara (due to inclination of the blade), the blade starts to rotate about the C.M. of the samara. This results in centrifugal forces being set up, and a more horizontal relative wind at the blade, and so the pitching angle and coning angle adjust to the equilibrium values as described in earlier sections of this paper. But because the C.M. of the whole samara lies near one end, the blade initially tends to swing towards a trailing position behind the C.M. It is only while the force of gravity is acting on the blade when this is in an inclined attitude, that it can contribute to starting autorotation, i.e. during the transient stage when the blade is swinging towards (or about) a trailing position.

(2) By the pressure of the air as the samara falls, the blade swings towards a trailing position behind the C.M. Because of the blade’s mass, there is an inertial force acting through the blade’s chordwise C.M., tending to oppose the angular acceleration of the blade. Because of this inertial force of the blade, the blade tends to adjust the angle of attack to the relative wind (just as in autorotation). Since the samara is falling vertically and its long axis forms an angle to the vertical, it is oblique blade sections ($a-a$ in Text-fig. 14) that adjust their angles of attack. Once the inherent angle of attack has been adjusted, the resultant aerodynamic force becomes tilted. Its lift component initially is horizontal (Text-fig. 14C). In this initial phase the samara does not rotate, or rotates only slowly, and the blade swings towards a trailing position, so the blade tip has as low a (or lower) relative air speed as has the proximal end. Therefore the spanwise C.P. is located near the geometric centre of the blade, not far distal to it as in autorotation. Since the C.P. of the blade lies lateral to the C.M. of the samara (due to inclination of the blade) the blade starts rotating about the C.M., and eventually the samara settles in autorotation.

If the swing of the blade towards a trailing position does not lead to autorotation as outlined above, the blade swings past the trailing position due to its angular momentum. When the swing then is retarded and the blade forced to swing back (due to the air pressure), inertial forces are again set up (due to retardation and subsequent acceleration in the reverse direction). Then the situation becomes again similar to that outlined above (Text-fig. 14 applies to both situations) and is likely to lead to autorotation.

Further, samaras are often ripped off the plant by winds, and then angular accelerations are set up, resulting in inertial forces which facilitate entering into autorotation.

V. SPANWISE CENTRE OF PRESSURE AND TOTAL FORCE COEFFICIENT OF THE BLADE

The spanwise C.P. is a point so located, that if the resultant aerodynamic force (the sum of all aerodynamic forces on the blade) acted through that point, it would produce the same moment about the centre of rotation of the samara as the distributed forces (Shapiro, 1955, p. 142).
Since the aerodynamic force of an aerofoil is proportional to the area of the aerofoil and the relative air velocity squared (other things being equal), the c.p. of the samara blade is located distal to the geometric centre of the blade. A strip analysis can be used to calculate the position of the spanwise c.p. The blade is then divided into $n$ narrow, chordwise strips (Text-fig. 17).

The total force coefficient of a wing $(C_L + C_D)$ is dependent on the wing profile and the angle of attack. In the case of the samara, the profile is almost identical over most of the blade, but the angle of attack decreases with increasing distance from the centre of rotation, and so the lift and drag coefficients $C_L$ and $C_D$ change along the span. All the resultant air forces of various strips probably do not lie on a vertical plane (the plane through the span axis of the samara and its axis of rotation) although the resultant force of the entire samara does. However, for a rough calculation of an average total force coefficient, the total force coefficient is assumed to be identical for all strips along the blade span. Further it is assumed that all the resultant air forces of the strips lie on a vertical plane through the span axis of the samara and its axis of rotation. Probably the errors introduced by these approximations are small. The distal part of the blade gives most of the force because of its high relative air speed, and in the distal part the approximations adopted probably do not deviate much from the true picture.

The sum $\Sigma F_R$ of the relative aerodynamic forces at all $n$ strips is given by the equation

$$\sum_{i=1}^{i=n} F_R = \sum_{i=1}^{i=n} A_i V_{res, i}^2$$

(22)

where $A_i$ is the area of strip $i$ and $V_{res, i}$ is the relative air velocity at strip $i$. $V_{res, i}$ is given by equation (10). (The forces in equation (22) and the moments in equation (23) are only relative since some factors necessary for calculation of absolute values are omitted, cf. equations (25) and (26).) The sum of the relative moments $\Sigma r_R$ of all $n$ strips about the c.m. of the samara is given by

$$\sum_{i=1}^{i=n} r_R = \sum_{i=1}^{i=n} r_i A_i V_{res, i}^2$$

(23)

where $r_i$ is the lever arm, which is the spanwise distance from the centre of rotation (c.m.) of the samara to the middle of strip $i$.

Thus the mean lever arm $r_{cp}$, which is the distance between the c.m. (centre of rotation) of the samara and the spanwise c.p. (Text-figs. 13, 17) is given by

$$\sum_{i=1}^{i=n} r_i A_i V_{res, i}^2 = r_{cp} \sum_{i=1}^{i=n} A_i V_{res, i}^2$$

(24)

where the left side is the sum of the relative moments of all $n$ strips (equation (23)) and the right side is the relative moment, obtained by multiplying the mean lever arm $r_{cp}$ with the resultant relative aerodynamic force obtained by summation of the relative forces at all strips (equation (22)). This method of calculation is similar to that used by Pennycuick (1967) with the modification given in Pennycuick (1968, p. 518). He
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used this method for calculation of the position of the spanwise C.P. of the wings of a pigeon in hovering flight.

In vertical autorotational descent the weight \( W \) of the samara is balanced by the vertical component of the total aerodynamic force of the blade. Because of the coning angle \( \beta \) the total aerodynamic force is equal to \( W/\cos\beta \) (Text-fig. 13).

The total force \( F \) of an aerofoil is given by

\[
F = \frac{1}{2}(C_L + C_D)\frac{1}{2}\rho AV^2,
\]

where \( C_L \) and \( C_D \) are the lift and drag coefficients (dimensionless), \( \rho \) is the air density, \( A \) the wing area, and \( V \) the relative air speed.

The mean total force coefficient \( (C_L + C_D)\frac{1}{2} \) of a samara blade may thus be calculated by equating the sum of the forces from all strips and the resultant force as expressed in terms of \( W \) and \( \beta \)

\[
\sum_{i=1}^{n} \frac{1}{2}(C_L + C_D)\frac{1}{2}\rho A_i V_{res, i}^2 = \frac{W}{\cos\beta},
\]

which may be rewritten as

\[
(C_L + C_D)\frac{1}{2} = 2W\int (\cos\beta \rho \sum_{i=1}^{n} A_i V_{res, i}^2).
\]

The total force coefficient obtained from equation (27) is an average one. Thus there are both worse and better coefficients along the blade span (depending on different angles of attack).

VI. STRUCTURE, FORM, AND FUNCTION

The most essential structural features of a samara are that it be a thin, flat, elongated (leaf-like) structure with the mass distributed in a special way, though not within very narrow limits. No twisting of the blade like the spanwise varied pitch of a propellor is needed.

(1) Mass distribution

By simple experiments it was found that the c.m. of the entire samara must lie between 0 and 30% of the span length from one end.

In order to keep the sinking speed low, the disk loading should be low (proportionality 5), i.e. the disk area swept by the blade should be large and the weight low. Thus the c.m. and hence the centre of rotation should be located as close to one end of the samara as possible, thereby giving a large radius to the disk. In samaras the c.m. usually lies 10-20% of the span axis from one end. For example, in *Acer pseudo-platanus* and *Picea abies* the fruit and seed, respectively, are rounded so that the proximal end of the samara does not function as an aerofoil, the c.m. thus lying outside the blade (Pl. 2 B and C). This favourable mass distribution depends on the low mass of the blade relative to the mass of the proximal end of the samara including the fruit or seed. In *Acer* and *Picea* the blade makes up ca. 15% of the total mass.

Apart from this spanwise mass distribution, the chordwise mass distribution must be such that the c.m. in chordwise strips over most of the blade is located 27-35% of
the chord behind one long side (cf. p. 571), which side thereby comes to be the leading edge in autorotation. Stability in the pitching plane, involving stability of the angles of attack and the gliding angles, is governed by the blade's profile shape and chordwise mass distribution (p. 571).

(2) Plan-form

The aerodynamic force increases with the aerofoil area and with the relative air velocity squared. Since the relative air velocity of a samara increases distally, blade area is made best use of far out from the centre of rotation. Hence the blade chord should increase distally.

On the other hand, there is the tip effect at the blade tip. The low pressure above the blade tends to be neutralized near the tip by air moving around the tip from the high-pressure region beneath the blade, giving rise to a trailing blade-tip vortex and accompanied induced drag (Text-fig. 15). Therefore a broad tip is of little use, so that blade material can be better used in making the blade longer or broader a bit from the tip. This probably is one reason why the blade plan-form tapers towards the tip.

If the spanwise aerodynamic and mass axes near the tip are to be kept coincident, the taper should converge on the one-third chord spanwise axis. The percentage taper then should be similar in the blade part in front of and behind the one-third-chord axis, leading to a much steeper taper at the trailing edge.

In the low Re number region in which samaras operate, the $L/D$ ratio decreases with the $Re$ number. Therefore the blade should be broad so as to contribute to a high $Re$ number and a high $L/D$ ratio.

Many samaras conform very well to this general plan-form, i.e. they have a broad blade that is broadest far out on the blade and its tip taper converges on the one-third-chord axis (Text-fig. 16, Pl. 2 A, B, C).

A positively raked tip (leading edge curving strongly backwards at the tip, leading edge shorter than the trailing edge) reduces pressure equalization at the tip and
thereby reduces drag (Weyl, 1945b). This tip shape involves a rearward displacement of the C.P. at the tip and therefore tends to give pitching moments. Samaras of a few species of plants have positively raked tips, as have the wings of many species of insects, for instance many fast anisopterous dragonflies (Pl. 2 D). In insects this shape of tip may be advantageous also for passive pitch-angle control at the tip.

(3) Structure

The concentration of ribs at the leading edge of the blade, as seen in for instance the samaras of *Acer* (Pl. 2 A, B) gives a rigid leading edge, which, however, is unnecessarily rigid in relation to the small aerodynamic stresses during autorotation. One important effect of this rib concentration is to give the proper chordwise distribution of mass.

The ribs (vascular bundles) pass outwards along the blade well concentrated at the leading edge. Successively, individual ribs branch off from the leading edge and bend sharply through large angles, *ca. 75°* in *Acer*, and continue towards the trailing edge with further branching and anastomosis and a pronounced taper.

This pattern of the ribs, following the leading edge outwards and then successively bending sharply backwards, provides a nearly maximal concentration of mass at the leading edge, which is indispensable for a proper chordwise mass distribution.

This rib pattern also makes the blade resistant to both lengthwise and chordwise bending and twisting.

Other functions of the vascular bundles are to give sustenance to the blade while this is growing, and also to retain the proper shape of the blade when drying. Samaras are usually shed from the plants only after having dried, and they then have a lower sinking speed because of lower disk loading.

The parallel orientation of ribs near the trailing edge does not prevent the trailing edge from becoming undulated when drying. However, this may promote a rapid entrance into autorotation (cf. p. 581).

The wings of most seeds lack ribs. Their proper chordwise mass distribution is obtained by varying the thickness of the membranous blade, which is thickest at the leading edge and becomes very thin towards the trailing edge (Pl. 2 C).
VII. DATA ON SAMARAS OF ACER PLATANOIDES AND PICEA ABIES

Data on the samara of *Acer platanoides* illustrated in Text-fig. 17 and Pl. 1B are given in this section to exemplify the dimensions, loads, and velocities involved. Performance data are from Pl. 1B. This samara and the others used from *Acer* were collected about the time in autumn when they were shed from the trees, and measurements and photographs were taken soon thereafter. The data thus apply to a relatively dry samara, as it is during the dispersal period.

A few data are given also for the small samara of *Picea abies*. Some of these data are mean values from several specimens. Performance data are from Pl. 1C.

<table>
<thead>
<tr>
<th></th>
<th><em>Acer platanoides</em></th>
<th><em>Picea abies</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length (cm)</td>
<td>4·7</td>
<td>1·4 (n=5)</td>
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<tr>
<td>Blade length (distance from c.m. to tip of blade) (cm)</td>
<td>3·7</td>
<td>1·1</td>
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<tr>
<td>Coning angle (°)</td>
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<td>22</td>
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<tr>
<td>Distance from c.m. to tip of blade measured normal to axis of rotation (cm)</td>
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<td>1·0</td>
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<tr>
<td>Maximal width (cm)</td>
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<td>0·7</td>
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<td>Samara area (one side) (cm²)</td>
<td>5·55</td>
<td>—</td>
</tr>
<tr>
<td>Blade area (part of samara distal to c.m.) (cm²)</td>
<td>4·52</td>
<td>0·45 (n=5)</td>
</tr>
<tr>
<td>Area of swept disk (projected on the tip path plane), $A_d$ (cm²),</td>
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<td>Blade area in percentage of disk area (solidity)</td>
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<td>Blade loading (N/m²)</td>
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<td>Disk loading, $W/A_d$ (N/m²)</td>
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<td>Rotation frequency, $f$ (rev/sec)</td>
<td>13</td>
<td>20</td>
</tr>
<tr>
<td>Angular frequency ($\omega = 2\pi f$) (rad./sec)</td>
<td>81·6</td>
<td>125·6</td>
</tr>
<tr>
<td>Sinking speed, $V_s$ (m/sec)</td>
<td>0·9</td>
<td>0·64</td>
</tr>
</tbody>
</table>

The following data apply to *Acer platanoides* except when otherwise stated. Final relative air speed, $V_f$: equation (4) gives:

$$0·332 - 0\cdot 52 = 0\cdot 9^2 - V_f^2, \quad V_f = 0\cdot 52 \text{ m/sec.}$$

Through-flow velocity $V_d$: equation (1) gives:

$$V_d = \frac{0\cdot 9 + 0\cdot 52}{2}, \quad V_d = 0\cdot 71 \text{ m/sec.}$$

Maximum downward speed of air in the shaft = $V_d - V_f = 0\cdot 9 - 0\cdot 52 = 0\cdot 38 \text{ m/sec.}$

Induced air speed at the disk = $\frac{V_d - V_f}{2} = \frac{0\cdot 9 - 0\cdot 52}{2} = 0\cdot 19 \text{ m/sec.}$

For calculation of the position of the spanwise c.p. and the average total force coefficient of the blade, a strip analysis was performed. The blade was divided into twelve chordwise strips, 3 mm broad, for which data are given in Table 1. The through-flow velocity was 0·71 m/sec and the perpendicular component $V_{dn}$ of this speed, at a coning angle of 20°, was $0\cdot 71 \cos 20° = 0\cdot 67 \text{ m/sec.}$ This value is used throughout in equation (10) for calculation of the resultant relative air speeds $V_{res, i}$. 
Text-fig. 17. Spanwise pressure distribution (total aerodynamic force, not its vertical component) of a samara of *Acer platanoides* in autorotational descent, calculated on the assumption that the total force coefficient \((C_L^2 + C_D^2)^{0.5}\) is constant along the blade and equal to 1.7 (cf. p. 590). Equation (25) used in the calculation. \(p = 1.22\). \(A\) and \(V^2\) taken from Table 1, column 7 \((A, V_{\text{cm}}^2)\). The samara is the one illustrated in Plate 1B and the one for which data appear in Table 1. The spanwise centre of pressure lies 66% of the blade span from the samara's centre of mass, c.M.

The sum values in Table 1, columns 7 and 8, are put into equation (24):

\[
r_{cp} = \frac{316.653 \times 10^{-7}}{12.987 \times 10^{-4}} = 0.0244 \text{ m.}
\]

The mean lever arm \(r_{cp}\) or the distance from the c.M. of the samara to its spanwise c.p., is 2.44 cm which is 66% (\(\frac{2}{3}\)) of the blade span from the c.M. The distance from the spanwise c.p. normal to the axis of rotation is equal to \(r_{cp}\cos\beta = 0.0229 \text{ m.}\)

The horizontal tangential speed at the c.p., \(V_{t,\text{cp}}\), is obtained from equation (8):

\[
V_{t,\text{cp}} = 81.6 \times 0.0229 = 1.869 \text{ m/sec.}
\]

Equation (10) gives the resultant relative air speed \(V_{\text{res, cp}}\) at the c.p.:

\[
V_{\text{res, cp}} = \sqrt{(0.67^2 + 1.869^2)} = 1.985 \text{ m/sec.}
\]

The gliding ratio at the spanwise c.p. (tangential, horizontal, speed at the c.p./perpendicular component of through-flow velocity) is \((1.869/0.67) = 2.8\). This corresponds to a gliding angle at the spanwise c.p. of 20°.

The ratio blade-tip tangential, horizontal, speed/sinking speed is \((2.86/0.90) = 3.2\),
Table 1. Data for 12 chordwise strips of a samara of Acer platanoides in autorotation, the one in Fig. 17 and Pl. 1B.

\( A_s \), strip area; \( r_{p} \), spanwise distance from the c.m. of the samara to the middle of the strip; \( r_{en} \), distance from the axis of rotation of the samara to the middle of the strip, measured normal to the axis of rotation; \( V_{t} \), tangential relative air speed (from equation (8)); \( V_{res} \), resultant relative air speed (from equation (10)); \( A_i V_{res} \), relative force at each strip; \( r_i A_i V_{res} \), relative moment of each strip about the c.m. of the samara. The relative, spanwise, pressure distribution is calculated on the assumption that the total force coefficient \((C_2 + C_2^b)\) is constant along the blade.

<table>
<thead>
<tr>
<th>Strip no.</th>
<th>( A_i ) (m²)</th>
<th>( r_{p} ) (m)</th>
<th>( r_{en} ) (m)</th>
<th>( V_{t} ) (m/sec)</th>
<th>( V_{res} ) (m/sec)</th>
<th>( r_i A_i V_{res} ) (x 10⁻⁴)</th>
<th>( r_i A_i V_{res} ) (x 10⁻⁴)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>30</td>
<td>1.5</td>
<td>1.4</td>
<td>0.114</td>
<td>0.680</td>
<td>0.139</td>
<td>0.208</td>
</tr>
<tr>
<td>2</td>
<td>30</td>
<td>4.5</td>
<td>4.2</td>
<td>0.343</td>
<td>0.753</td>
<td>0.170</td>
<td>0.765</td>
</tr>
<tr>
<td>3</td>
<td>33</td>
<td>7.5</td>
<td>7.0</td>
<td>0.561</td>
<td>0.860</td>
<td>0.256</td>
<td>1.917</td>
</tr>
<tr>
<td>4</td>
<td>39</td>
<td>10.5</td>
<td>9.9</td>
<td>0.808</td>
<td>1.050</td>
<td>0.430</td>
<td>4.511</td>
</tr>
<tr>
<td>5</td>
<td>44</td>
<td>13.5</td>
<td>12.7</td>
<td>1.036</td>
<td>1.234</td>
<td>0.670</td>
<td>9.040</td>
</tr>
<tr>
<td>6</td>
<td>47</td>
<td>16.5</td>
<td>15.5</td>
<td>1.265</td>
<td>1.431</td>
<td>0.963</td>
<td>15.887</td>
</tr>
<tr>
<td>7</td>
<td>48</td>
<td>19.5</td>
<td>18.3</td>
<td>1.493</td>
<td>1.636</td>
<td>1.285</td>
<td>25.063</td>
</tr>
<tr>
<td>8</td>
<td>46</td>
<td>22.5</td>
<td>21.1</td>
<td>1.722</td>
<td>1.848</td>
<td>1.570</td>
<td>35.334</td>
</tr>
<tr>
<td>9</td>
<td>43</td>
<td>25.5</td>
<td>24.0</td>
<td>1.958</td>
<td>2.069</td>
<td>1.841</td>
<td>46.956</td>
</tr>
<tr>
<td>10</td>
<td>39</td>
<td>28.5</td>
<td>26.8</td>
<td>2.187</td>
<td>2.287</td>
<td>2.040</td>
<td>58.149</td>
</tr>
<tr>
<td>11</td>
<td>32</td>
<td>31.5</td>
<td>30.0</td>
<td>2.448</td>
<td>2.538</td>
<td>2.061</td>
<td>64.928</td>
</tr>
<tr>
<td>12</td>
<td>21</td>
<td>34.5</td>
<td>32.4</td>
<td>2.644</td>
<td>2.728</td>
<td>1.562</td>
<td>53.956</td>
</tr>
<tr>
<td>Sum</td>
<td>452</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>12.987</td>
</tr>
</tbody>
</table>

corresponding to a tip-path inclination of 17.5°. In Picea abies this ratio is 2.1 and the tip-path inclination is 26°.

Equation (27) gives the total force coefficient (values from data above and from Table 1):

\[
(C_2^p + C_2^b)^\frac{1}{4} = \frac{2 \times 0.00013 \times 9.81}{0.9397 \times 1.22 \times 12.987 \times 10^{-4}} = 1.7.
\]

The spanwise aerodynamic force distribution of the blade is calculated with the value 1.7 for the total force coefficient. The result is plotted in Text-fig. 17. The outer one-third of the blade contributes half of the total aerodynamic force.

The \( Re \) number is given by

\[
Re = \frac{V_{res} l_c}{\nu},
\]

where \( V_{res} \) is the resultant relative air speed, \( l_c \) is the chord length, and \( \nu \) is the kinematic viscosity of the air, obtained from the ratio viscosity \( \eta/\rho \) of the air \((\nu = \eta/\rho = 15 \times 10^{-6} \text{ m}^2/\text{sec})\). \( V_{res} \) at the spanwise c.p. of the samara blade is 1.985 m/sec, \( l_c \) is 0.015 m, and the \( Re \) number at the spanwise c.p. of the samara blade is \((1.985 \times 0.015 \times 10^9/15) = 2000\).

For the samaras of Picea abies the \( Re \) number at \( \frac{3}{4} r \) is ca. 500.

There are notable differences between individual samaras in the ratio blade-tip tangential speed/sinking speed. Some of the Acer samaras photographed performed
somewhat better than the one for which data are given above. Further, a samara that is bent usually performs in a different way depending on which side is up.

VIII. DISCUSSION AND COMPARISONS WITH ANIMAL FLIGHT

From the data given above for an *Acer* samara it is seen that the air in the shaft is accelerated downwards to a speed of about 0.4 \( (V_a - V_j)/V_a = 0.38/0.90) \) of the sinking speed of the samara. The ratio of the air velocities relative to the samara behind and in front of the disk is 0.6 \( (V_j/V_a = 0.52/0.90) \). The data on sinking speed and induced air speeds agree very well with those given by Hertel (1966, p. 91) for dry samaras of *Acer platanoides*.

The blade of a samara functions essentially as an aerofoil, i.e. the lift force is the largest force. However, the drag force is about one-third the lift force in *Acer*, and about half the lift force in *Picea*, and gives a useful contribution to the resultant air force.

The samara operates at low Re numbers and therefore is bound to have low \( L/D \) ratios. The average \( L/D \) ratio of the blade of the *Acer* samara above is of the order of 3 and hence falls in the same region as that of the wings of medium-sized and large insects. The much smaller samara of *Picea*, operating at lower Re numbers, also has a lower \( L/D \) ratio, ca. 2, as indicated by the tip-path inclination (see p. 590).

As examples of insects, the forewing of *Catocala* sp. (*Lepidoptera, Noctuidae*) was found by wind-tunnel measurement to have a maximum \( L/D \) ratio of 2.8 at a Re number of \( 3 \times 10^3 \) (Nachtigall, 1967). In the locust *Schistocerca gregaria* Forskål the best gliding ratio and hence \( L/D \) ratio of the whole animal is 6.5 (Jensen, 1956).

In a comparison between performance data of samaras and birds it should be noticed that they operate at very different Re numbers, about \( 2 \times 10^8 \) for samaras (of *Acer* size) and \( 3 \times 10^4 \) to \( 3 \times 10^6 \) for birds (Hertel, 1966, p. 234; Parrott, 1970; Pennycuick, 1967). In birds the best \( L/D \) ratios of the whole animal lie between 5 and 12 (Parrott, 1970).

In some gliders (sailplanes) on the other hand, the \( L/D \) ratio is about 40 for the whole plane and about 100 for the wing only at Re numbers of about \( 1.0 \times 10^6 \).

The total force coefficient \( (C_L + C_D) \) of a samara of *Acer platanoides* was calculated to be 1.7.

Jensen (1956) calculated lift coefficients of the forewing of *Schistocerca gregaria*. The wing was located near the wall of a wind tunnel, thus being immersed in a graded wind flow simulating the graded relative wind past the wing of a flying insect. When the wing was flat, \( C_{L,\text{max}} \) was 1.1, whereas it amounted to 1.3 when the wing was cambered by deflecting the rear part \( 25^\circ \).

In hovering flight the pigeon *Columba livia* reaches a lift coefficient of 2.8, and in gliding flight the maximum lift coefficient of the pigeon and of the dog-faced bat *Rousettus aegyptiacus* (E. Geoffroy) is about 1.5 (Pennycuick, 1968, 1971). The maximum lift coefficient in gliding flight of the falcon *Falco jugger* is 1.6 (Tucker & Parrott, 1970), and that of the vulture *Coragyps atratus* 1.1 (Parrott, 1970).

Since the samara blade operates at such low Re numbers and does not have a
cambered blade profile, its total force coefficient of 1.7 stands out as a bit high. This high value might indicate that the flow pattern through the disk of the autorotating samara is intermediate between the windmill state (which state was assumed in this calculation of the total force coefficient) and the ideal limiting case of zero throughflow, namely the turbulent windmill state or parachute state. Descriptions of these flow patterns are given in Shapiro (1955, p. 9) and McCormick (1967, p. 117).

The sinking speed of a samara is similar to or slower than that of most birds in gliding flight. It is about 0.9 m/sec in Acer samaras and usually about 1 m/sec or more in birds, varying with the flight speed (Parrott, 1970; compilation of data from several authors).

The wing (blade) loading of Acer samaras is ca. 2.8 N/m², whereas it is 10–200 N/m² in birds (Greene, 1962). The relatively bad L/D ratio of the samara is compensated by a low blade loading, thus making low sinking speeds possible.

Schistocerca gregaria (the whole insect) has a minimum sinking speed of 0.6 m/sec in gliding flight (Jensen, 1956), which is equal to the sinking speed of a Picea samara and somewhat less than that of Acer samaras.

A flat disk and an open hemisphere (parachute) with the same mass as the Acer samara above and the same circular area and opening area, respectively, as the disk swept by the Acer samara, would have sinking speeds of ca. 0.72 and 0.65 m/sec, respectively, as read from fig. 116 in Hertel (1966). Thus, the samara has a sinking speed 125% of that of a flat disk and 138% of that of an open hemisphere.

In this comparison it should be considered that the samara blade makes up only 12% of the disk area that it sweeps (Text-fig. 7). Further, a fruit-carrying flat plate or an open hemisphere, the size of the disk swept by the samara, would require more biomass and would also need some stabilizing device. Therefore, the samara stands out as a simple and very efficient structure in braking the sinking speed of the diaspore.

(1) Comparative remarks on samara blades and insect wings

The spanwise torsion axis, or elastic axis of support, of an insect wing is the spanwise axis through which the force of the wing-beat muscles act. Thus, if a resistance to the beating of the wing is applied on the torsion axis, no pitching moment of the wing is produced. This elastic axis (= torsion axis) is the functional equivalent to the mass axis (= torsion axis) of the samara blade.

The position of the spanwise torsion axis in insect wings is determined by the wing base geometry and the stiffness distribution of the wing. The stiffness distribution depends on the venation pattern. In most insects there is a concentration of strong, longitudinal, supporting veins in the anterior part of the wing. In the posterior part of the wing there are weaker veins, that bend towards the trailing edge. This general pattern of venation in insect wings resembles the pattern of vascular bundles in a samara blade. The objective of making the wing (blade) resistant to longitudinal and chordwise bending and to twisting is common to both structures. The insect wing, however, is very much lighter than the samara blade, and accordingly has a more efficient structure, often including pleating patterns, to make the wing rigid.

In samara blades the mass axis, aerodynamic axis, and torsion axis coincide. In
many insect wings they do not. Usually the torsion axis is located ahead of the mass and aerodynamic axes in insect wings.

Because the wings flap, the local direction of the relative wind is different along the wing. In order to maintain proper angles of attack along the span, the wing needs to be twisted. Wing twisting becomes more important the larger the insect. In the small insect *Drosophila* there is no lengthwise wing twisting, nor is there any need of it since its wings are almost un stallable (Vogel, 1967a, b).

In wings having the torsion axis located ahead of the aerodynamic axis, there is a couple giving a torsion moment (increasing with the distance from the wing hinge). This tends to twist the wing until an equally large opposing moment builds up caused by the elastic deformation of the wing supporting structures. Hence, lengthwise wing twisting, involving adjustment of angles of attack relative to the local relative winds along the wing, in some insects may be achieved (at least partly) in a passive way because of the location of the torsion axis ahead of the aerodynamic axis.

In many insects, however, wing twisting has been shown to be largely under neuromuscular control via the sclerites operating the wing. This applies, for instance, to *Aeschna* dragonflies (Neville, 1960) and to the forewings of *Schistocerca gregaria*, but deformation of the hindwings of the latter is determined largely by aerodynamic forces (Weis-Fogh, 1956; Jensen, 1956; Gettrup & Wilson, 1964; Gettrup, 1966).

When the chordwise c.m. lies behind the torsion axis, the wing is very susceptible to self-excited, coupled, flapping and feathering oscillations (flutter) in passive flight. Also in active flight this position of the mass and torsion axes gives unfavourable pitching moments.

In many insects there is a mass concentration far out on the leading edge of the wing in the form of the pterostigma. It seems to have the functions of raising the critical speed above which flutter occurs in passive flight, and also of suppressing unfavourable pitching moments in active flight, simply by moving the chordwise c.m. forwards (Pl. 2 D) (Norberg, 1972).

**IX. SUMMARY**

1. A samara is a winged fruit or seed that autorotates when falling, thereby reducing the sinking speed of the diaspore and increasing the distance it may be transported by winds. Samaras have evolved independently in a large number of plants.

2. Aerodynamical, mechanical, and structural properties crucial for the inherent self-stability are analysed, and formulae for calculation of performance data are given.

3. The momentum theorem is applied to samaras to calculate induced air velocities. As a basis for blade element analysis, and for directional stability analysis, various velocity components are put together into resultant relative air velocities normal to the blade's span axis for a samara in vertical autorotation and also in autorotation with side-slip.

4. When falling, a samara is free to move in any sense, but in autorotation it possesses static and dynamic stability. Mainly qualitative aspects on static stability are presented. Simple experiments on flat plates at Reynolds numbers about 2000 as in samaras, showed that pitch stability prevails when the c.m. (centre of mass) is located
27–35\% of the chord behind the leading edge. The aerodynamic c.p. (centre of pressure) moves forward upon a decrease of the angle of attack, backward upon an increase. In samara blades the c.m. lies ca. one-third chord behind the leading edge, and hence the aerodynamic and centrifugal forces interact so as to give pitch stability, involving stability of the angles of attack and gliding angles.

5. Photographs show that the centre of rotation of the samara approximately coincides with its c.m.

6. The coning angle (blade angle to tip path plane) taken up by the samara is determined by opposing moments set up by the centrifugal and aerodynamic forces. It is essentially the centrifugal moment (being a tangent function of the coning angle, which is small) that changes upon a change of coning angle, until the centrifugal and aerodynamic moments cancel out at the equilibrium coning angle.

7. Directional stability is maintained by keeping the tip path plane horizontal whereby a vertical descent path relative to the ambient air is maintained. Tilting of the tip path plane results in side-slip. Side-slip leads to an increased relative air speed at the blade when advancing, a reduced speed when retreating. The correspondingly fluctuating aerodynamic force and the gyroscopic action of the samara lead to restoring moments that bring the tip path plane back to the horizontal.

8. Entrance into autorotation is due to interaction between aerodynamic forces, the force of gravity, and inertial forces (when the blade accelerates towards a trailing position behind the c.m. of the samara).

9. The mass distribution must be such that the c.m. lies 0–30\% of the span from one end. In Acer and Picea samaras the c.m. lies 10–20\% from one end, thereby making the disk area swept by the blade large and the sinking speed low.

10. The blade plan-form is discussed in relation to aerodynamics. The width is largest far out on the blade where the relative air velocities are large. The large width of the blade contributes to a high $Re$ number and thus probably to a better $L/D$ (lift/drag) ratio and a slower descent.

11. The concentration of vascular bundles at the leading edge of the blade and the tapering of the blade thickness towards the trailing edge are essential for a proper chordwise mass distribution.

12. Data are given for samaras of Acer and Picea, and calculations of performance are made by means of the formulae given in the paper. Some figures for an Acer samara are: sinking speed 0.9 m/sec, tip path inclination 15°, average total force coefficient 1.7 (which is discussed), and a $L/D$ ratio of the blade approximately 3.

13. The performances of samaras are compared with those of insects, birds, bats, a flat plate, and a parachute. They show the samara to be a relatively very efficient structure in braking the sinking speed of the diaspore.

14. In samaras the mass, aerodynamic, and torsion axes coincide, whereas in insect wings the torsion axis often lies ahead of the other two. Location of the torsion axis in front of the aerodynamic axis in insects tends towards passive wing twisting and passive adjustment of the angles of attack relative to the incident air stream, the direction of which varies along the wing because of wing flapping.

15. Location of the mass axis behind the torsion axis may lead to unfavourable
Autorotation, self-stability, and structure of samaras

wing pitching moments in insects. This seems to be counteracted in many insects by a concentration of mass, the pterostigma, far out on the leading edge of the wing.

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X. REFERENCES


EXPLANATION OF PLATES

PLATE I

(A) A samara of maple, Acer platanoides, entering into autorotation. Due to autorotation the sinking speed is reduced to one-sixth of the maximum speed before autorotation. 100 exposures/sec. (B) A samara of A. platanoides in autorotation. 100 exposures/sec. (C) A samara of spruce, Picea abies, in autorotation. 100 exposures/sec.
Winged fruit of (A) maple, *Acer platanoides* (transmitted light) and (B) sycamore, *A. pseudoplatanus*, (reflected light). (C) Winged seed of spruce, *Picea abies* (transmitted light). The white mark on the samaras indicates the position of the c.m. The localization of the c.m. of the whole samara close to one end is due to the localization of the fruit or seed close to one end and to the thickness of the structures covering the fruit or seed. The localization of the c.m. of chordwise strips of the blade *ca.* one-third chord length behind the leading edge is due to the concentration of vascular bundles at the leading edge of *Acer* samara blades. In the membranous *Picea* samara blade this chordwise mass distribution is due to a thickness gradient from the leading edge towards the trailing edge (see the samara blades in transmitted light, (A) and (C)). These are the functionally most important structural characteristics of samaras. (D) Forewing and hindwing of the dragonfly *Aeschna grandis* L. with the torsion axis and the chordwise position of the c.m. of wing strips (broken lines) indicated. Distance of centre of mass behind leading edge is given as percentage of chord length for each strip. A wing having its chordwise centre of mass located behind its torsion axis (as in (D)) is susceptible to self-excited flutter in gliding flight and unfavourable pitching moments in active flight. The pterostigma (the dark structure at the leading edge near the wing tip) adds mass to the leading edge and hence suppresses flutter in gliding flight and unfavourable pitching moments in active flight. Differences between samara blades and insect wings are discussed in the text with special regard to the position of the torsion and mass axes (cf. Text-fig. 16) and to tip shape.
Aeschna grandis

R. AKE NORBERG